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BIOLOGICAL BULLETIN

THE DETERMINATION OF DOMINANCE AND THE MODIFICATION OF BEHAVIOR IN ALTERNATIVE (MENDELIAN) INHERITANCE, BY CONDITIONS SURROUNDING OR INCIDENT UPON THE GERM CELLS AT FERTILIZATION.¹

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INTRODUCTION.

The Point of View.—The mutation theory of DeVries, the rediscovery of Mendel's paper on hybrid peas, and the work of the Mendelian hybridologists have focused the attention of biologists upon the characters of organisms as basal units for investigation in the effort to understand the *modus operandi* of evolution. The most conspicuous outcome is the growth of the "unit character" hypothesis, which, in the main, has been adopted by the Neo-Mendelians as the fundamental assumption necessary

¹A paper presented at the meeting of the American Naturalists in Boston, Dec., 1909.

for their practice and theory, because of the fact that the characters of organisms often stand out sharply and behave with distinctness in the processes which follow reproduction.

That many of the characters in organisms are distinct and behave in the sharp, alternative fashion described by the Mendelians, there can be no reasonable doubt. To deny the existence of these sharply defined, predicable behaviors in inheritance is to deny the evidence of our senses, and accuse a considerable body of reputable workers of inability to make accurate observations. *The fundamental question is, do these unit characters, or lesser entities, occupy in the organism the mosaic relation and have the capacity for the mosaic rearrangement which is assumed by most Mendelians and by the followers of De Vries?*

We must not be diverted from the main question by any fancied injury to our biological orthodoxies by the Neo-Mendelians' array of factors, determiners, allelomorphs, gametic couplings, latencies, etc., *because these represent only the symbols of processes at present unknown, although the results of these unknown processes are observable, predicable, capable of control and modification.*

Many, unable to accept the consequences which they believe to be the logical outcome of the unit character conception and the mosaic composition of organisms, take refuge in speculations in which the organic individual is compared to inorganic crystals, and state their position as follows:

In the inorganic world the attributes and qualities of a particular substance are due to the interaction of the component molecules and atoms, resulting in manifestations of one kind or another, which, as far as the mass is concerned, are essentially equivalent to the characters found in organisms. That is to say, in a crystal of copper sulphate the crystalline form and blue color are not due to a series of representative particles, or to unit characters, but they are due to the arrangement of the component molecules of copper sulphate and water of crystallization; in short, to a host of complex interactions of the component molecules. Copper sulphate crystals, in order to retain their specific identity, must consist of a definite proportion and arrangement of these molecules, and there is no *à priori* reason why it is any

different in organisms, unless we assume that there is in living substance something fundamentally different from that of non-living matter, and any such admission at once commits the maker thereof to vitalism.

I am not convinced that the analogy between a crystal and an organic individual is justified. This idea, of which Haeckel is the foremost exponent—while it has points in its favor—leaves much unexplained, and in living substance there are many processes and attributes which can be taken away, *i. e.*, are absent as far as perception is concerned, leaving a similar mass with other attributes.

There is much justification for considering organic species in the same light as we view non-living species. Thus a granite rock is as distinctive and specific as any animal or plant species. It has properties, attributes of the whole and also specific characters of the component parts. The basal components—orthoclase-feldspar, mica, quartz—exist in crystalline form in a granular crystalline complex; while the whole has specific attributes and qualities, the products of the interactions of the component parts and of the forces incident upon the elementary component substances at the time of combination. Depending upon variations of the mica—whether muscovit or biotite—and upon the amount and size of the mica masses, the appearance and attributes of the granites change; and much also depends upon whether the feldspar is orthoclase-feldspar or triclinic-feldspar, etc.

The possible number of specific kinds of granite is very considerable and depends solely upon the nature of the component substances and the conditions under which the combinations are effected, while the specific end products are as distinctive as any plant or animal form.

Likewise in feldspar, (a rock-forming unit character?) the crystalline form depends upon what it is that is combined with the silicates of aluminum, whether salts of calcium, sodium, potassium or barium, to give the range of color, form, hardness, cleavage, specific gravity, etc., found in the feldspar. Feldspar is crystalline, has polarity, and might well be a parallel to an organic form, but the constituent substances can be changed, replaced, giving distinct, specific end results. In orthoclase, which

is a potash feldspar, is the potash a mineralogical unit character? It seems to me that the problem of the constitution of natural substances is the same in both living and non-living substance, and that there is in living substance something very much like that which is found in non-living substance in the combining of attributes from diverse sources into compact and distinct wholes.

Because a character is sharp and distinct, or may be apparently removed, is no necessary reason for supposing that it may be taken away as an entity, and no reason whatsoever for believing it to be conditioned by a subsidiary mass; rather, we must regard an organism essentially as we would look upon any inorganic substance, as a mass of matter in which the unit is the individual with its array of attributes or qualities, or its specific characters. It is certain, however, that there is adequate evidence to prove the truth of the situation as described by the Mendelians as far as the behavior of the attributes is concerned; but the basis and cause of this behavior is entirely unknown, and must remain unknown until we have replaced by fuller knowledge the present crude ideas of the constitution of living substance.

The situation which has developed in the last few years at the hands of the Neo-Mendelians themselves is interesting.

From the simple conditions discovered by Mendel there has arisen through the work of the last decade an array of observations tending to show that the Mendelian phenomenon is not in many instances as distinct and simple as one might wish, and at present divers kinds of variability in the behavior of characters are described and attributed, in some instances, to several different kinds of latency, to gametic coupling, to variable potency, to variable dominance, and so on. The situation essentially is this, that as investigation has progressed it has been discovered that not one, but a host of determining factors (I use the word factor as meaning something which makes possible a given result, with no idea expressed or implied as to the nature of this factor) are operative in the production of alternative inheritance; and in the attempt to preserve the letter of the law of Mendelian theory of unit characters with segregation in gametogenesis, a host of hypotheses have been developed in order to save the original theory.

Among the Neo-Mendelians the assumption is universal that all the differences that come out of crosses are entirely due to internal factors brought into the fertilized egg by the gametes as factors and determiners, to various combinations of allelomorphs, and so on. That some of these variable conditions may be due to external causes does not seem to have occurred to any of the Mendelians, and no effort has been made to eliminate in any one case what would first be eliminated in any accurate physical or chemical work, namely, the effect of surrounding conditions, and forces incident upon the reactions unquestionably going on in the developing individual.

Probably most of us will admit that the fertilization process represents the bringing together of two more or less like physico-chemical masses, and the combining of these into a new body with potentialities and capacities which then enable it to go on in a constantly increasing series of epigenetic reactions, and ontogenetic processes, and finally to evolve into an adult organism. The essence of the activity and reaction involved are beyond any question physico-chemical in their nature. This being true, the first step in the elucidation of this complex array of variability in behavior is to determine to what extent surrounding or incident forces may modify in a particular case the type of alternative inheritance which is found; when effects of these forces are known, then attack can be profitably made upon problems of internal factors. This first step I have in part accomplished in a series of experiments which form the basis of this preliminary paper.

Material.—The material upon which this series of experiments herein described was carried out consisted of three species of chrysomelid beetles of the genus *Leptinotarsa*, which would hybridize freely and perfectly in all directions: *Leptinotarsa signaticollis* Stål, a species occurring in southern Mexico at the foot of the escarpment on the western side of the Mexican plateau; *Leptinotarsa undecimlineata* Stål, a species confined entirely to the savannahs and lower foot hills from Tampico in Mexico, southward to Costa Rica and Panama; and *Leptinotarsa diversa* n. sp., which is very similar to the former but is limited entirely to the higher foot hills on the border of the Mexican plateau. The reason for

choosing these three species was that any two of them, when crossed, give only certain very definite and invariable products, and I was thus enabled to eliminate many complications and possible sources of error. The contrasting characters are as follows:

Between *L. signaticollis* Stål (Fig. 1) and *L. undecimlineata* Stål (Fig. 2), in the adult, the elytra of *L. undecimlineata* have deep greenish black longitudinal stripes, edged with a double row of punctations, while *L. signaticollis* has the punctations, but not the stripes. The ground color of the elytra in *L. signaticollis* is grayish, while in *L. undecimlineata* it is white. No other characters in the adult had sufficient contrast to give sharp alternative inheritance. The larvæ of the two are sharply contrasted; those of *L. undecimlineata* and *L. signaticollis* are exactly



FIG. 1. *L. signaticollis* Stål. (A) Adult. Showing the absence of pigment, and the presence of the impressed punctations on the elytra which border the stripes in other species. The absence of pigment may well represent the negative half of a Mendelian allelomorph. (B) Full-grown larva. Showing the arrangement of black color marks upon the sides and back of the larvæ. The ground color in this state is bright chrome yellow. (C) Larva of second stage. Showing the characteristic color pattern. The ground color is a light chrome yellow.

alike in the first stage, but in the second stage *L. undecimlineata* is white and *L. signaticollis* yellow, both with the same system of spots, and in the third stage *L. signaticollis* is yellow with well-developed tergal stripes and *L. undecimlineata* is pure white without stripes. These differences are well shown in text Figs. 1 and 2.

In *L. diversa* (Fig. 3) the elytra are marked by longitudinal stripes of greenish black edged with an irregular double row of punctations, and the larvæ are in all stages exactly like those of

L. signaticollis. There are no other simple differences between the three species that could be readily utilized in experiments of this kind, but the characters used are sharp and striking, and satisfy in every respect the conditions demanded by Mendelian hypotheses.

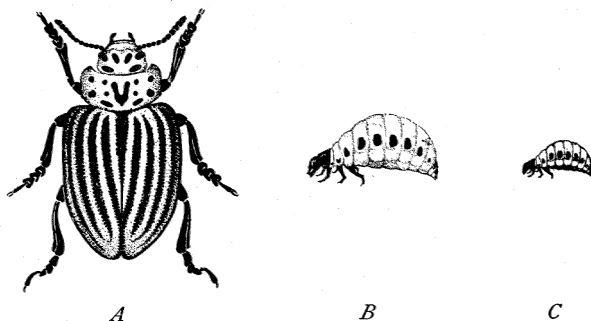


FIG. 2. *L. undecimlineata* Stål. (A) Adult. Showing on the elytra the presence of longitudinal pigmented bands which are bordered by rows of punctations as in *L. signaticollis*. The pigmented bands may be considered the positive half of a Mendelian allelomorph, so that when the two species are crossed we are following all of the Mendelian qualifications in crossing the presence and absence of the same character. (B) Full-grown larva, showing the characteristic color pattern in this stage. The ground color is pearly white. (C) Second stage larva, showing the characteristic color pattern. The ground color is also pearly white.

The elytral stripes of *L. diversa* and *L. undecimlineata* represent the present or positive character, and the lack of stripes in *L. signaticollis* the absence or negative factor of an allelomorphic pair, the yellow hypodermal color one member and the white the other of an allelomorphic pair: yl = (+) wh = (-); the dorsal spots the presence (+) and their absence the absence a(-) of another pair of allelomorphs—when we view the characters from the present Neo-Mendelian standpoint.

A further reason for choosing this material for this investigation is the fact that when crossed it often gives most perfect Mendelian results, and in some cases perfect ratios of 1:2:1 are obtained in the second hybrid generation, while other crosses, brothers and sisters of the same material, did not give the same, but on the contrary, quite different results. For some time I was at a loss to understand the reason for this anomalous condition. No amount of crossing or investigation succeeded in disclosing

the presence of any internal factor, which by its operations would produce this result. Careful examination, however, of the records which have been kept in the vivarium where these experiments were carried on, gave evidence that the differences were possibly due to the conditions surrounding the hybrid series during development. Accordingly, an array of experiments has



FIG. 3. *L. diversa*. (A) Adult. Showing the presence on the elytra of longitudinal dark stripes in exactly the same position as the dark stripes in *L. undecimlineata*, and in the position of the absence of stripes in *L. signaticollis*. (B) Full-grown larva, showing characteristic color pattern. The ground color is bright chrome yellow as in *L. signaticollis*. (C) Second stage larva, showing characteristic color pattern. The ground color is yellow.

been carried out to test this point—do the conditions surrounding or incident upon the gametes before and at fertilization and in early ontogeny influence in any way the behavior of characters? As far as this phase of the modifiability of alternative inheritance is concerned, I have essayed to investigate it in two ways: first, by the usual process of hybrid analysis, as it is practiced in all Mendelian work, in which the extracted dominants, recessives and heterozygous forms are isolated and carried on as pure cultures, and again inbred and tested in the usual ways—essentially experiments in analysis to determine germinal constitution; second, I have carried on a series of complicated experiments in synthesis, comparable to those which one would expect to go on in nature when two of these species are brought into contact and hybridized, in order to learn what the result would be if two species should come in contact under different conditions, and hybridize, and these results I shall describe under the head of Experiments in Synthesis.

EXPERIMENTS IN ANALYSIS.

Crosses Between L. signaticollis and L. diversa.

The first effort was to determine whether or not external or incident conditions were in any way responsible for the production of the diversity of behavior found. The first experiment was a cross between a male *L. diversa* and a female *L. signaticollis*.

L. signaticollis ♀ × ♂ *L. diversa*.

Exp. No. H 409.¹

A virgin female of *L. signaticollis*, from Exp. No. 419, g. XI (CCB) was mated with a male *L. diversa*, from Exp. No. 816, g. VI (A), under the following conditions:

FOOD : NORMAL — UNIFORM.

T.		R. H.	
Day Av.	80° F. ± 5°.	Day Av.	75 per cent. ± 5 per cent.
Night Av.	75° F. ± 8°.	Night Av.	75 per cent. ± 5 per cent.

In the F_1 generation the larvæ were all alike, as was to be expected since the larval stages of the parental stocks are similar. These larvæ gave rise to F_1 hybrid adults distributed in two sharply marked groups. One of these groups was indistinguishable from the female parent stock, and the other was an intermediate between the male and female parental stocks, in which the essential contrasting character between the adults was in the elytral stripes and these were distinctly midway between the two parent types, (a blend). The numbers were 49 of the *signaticollis* type (sig. type), to 53 of the mid type (mid type)—practically a 1:1 ratio.

Several pairs of each of these types were mated for the F_2 generation. The matings of the *signaticollis* type gave in the F_2 generation pure *signaticollis*, and further breeding for five consecutive generations gave only *signaticollis* types. The progeny of the mid type, however, split in the F_2 generation into three classes, with perfect Mendelian ratios, one like the female *signaticollis* type, one like the male *diversa* type, and the mid type. For example, pair A, gave:

sig. type.	mid. type.	diversa type.
observed 59 :	121 :	61.
expected 60.25	120.50	60.25

¹ These experiment numbers are those of the original records, which are now attached to the specimens preserved as a record of this work.

The extracted forms of the *signaticollis* type, when inbred, continued to breed true in F_3 ; the extracted forms like the male *diversa* type likewise came true in F_3 , F_4 and F_5 ; and the mid types in generations F_3 and F_4 gave in all cases close approximations to the ratio 1:2:1. The behavior observed in experiments of this class is shown in Plane I., a digest of Exp. No. H 409.

This behavior would suggest that either one or the other of the parents used was a "heterozygous form." When, however, identical material, brothers and sisters of the first, were reared under other conditions, a different result was obtained.

L. signaticollis ♀ × ♂ *L. diversa*.

Exp. No. H 410.

In Plate II. are represented the results obtained in crossing a female *L. signaticollis* and a male *L. diversa* of exactly the same stocks as described in Exp. No. H 409, but under the following conditions:

FOOD : NORMAL — UNIFORM.

T.		R. H.	
Day Av.	75° F. ± 5°.	Day Av.	50 per cent. ± 10 per cent.
Night Av.	50° F. ± 5°.	Night Av.	80 per cent. ± 15 per cent.

In the F_1 generation of this experiment there was one class of adults, invariably of the mid type, and these, when inbred, gave in the F_2 generation a typical Mendelian grouping of types, in the majority of cases in as nearly perfect ratio of 1:2:1 as could be desired. These two crosses were repeated eleven times under the same conditions with the same results, the only variation being a slight oscillation in the 1:2:1 ratio of the F_2 generation and a slight variation in the mid types. The number of pairs that have been used would in itself be sufficient evidence that the results were not due to the chance selection of individuals which would give these results, but that they were due entirely to the conditions surrounding the germinal materials at the time of their combination and during their early development. To still further test the point, a more crucial experiment was carried out as follows:

L. signaticollis ♀ × ♂ *L. diversa*.

Exp. No. H 409/411.

A female of *L. signaticollis* and a male *L. diversa* were allowed to reproduce under the conditions of the first experiment (Exp. No. H 409), while a certain number of their eggs were being laid (designated as Lot A). These eggs developed normally under the following conditions:

FOOD : NORMAL — UNIFORM.

T.		R. H.	
Day Av.	80° F. ± 5.4°.	Day Av.	74 per cent. ± 6 per cent.
Night Av.	75° F. ± 7.8°.	Night Av.	75 per cent. ± 5.7 per cent.

and gave typical larvæ, which gave two classes of adults in the F₁ generation in the proportion of approximately 1:1, or

sig. type.	mid type.
88 :	94.

The individuals like the female parent (sig. type), when inbred, came true to the type for four consecutive generations, which was as far as they were carried; while the mid types, when inbred, gave in the F₂ generation marked Mendelian ratios in the proportion of 1:2:1, the numbers for Pair B being:

<i>signaticollis</i> type	mid type.	<i>diversa</i> type.
Observed 98 :	201 :	101.
Expected 100 :	200 :	100.

After a few days the same pair of individuals was placed under the conditions of Exp. No. H 410:

FOOD : NORMAL — UNIFORM.

T.		R. H.	
Day Av.	± 75° F. 4.3°.	Day Av.	51.2 per cent. ± 11 per cent.
Night Av.	± 51° F. 5.8°.	Night Av.	81.5 per cent. ± 14.2 per cent.

and there allowed to develop another set of eggs (Lot B).

These eggs developed normally and gave in the F₁ generation only a single type like the *signaticollis* parent, which, when inbred, gave in the F₂ generation *signaticollis*, and continued to breed true for four consecutive generations. This experiment was repeated seven times with uniform results, confirming the

conclusions drawn from the first two experiments and showing beyond doubt that the variability of behavior in the alternative inheritance of the elytral stripes in these two species of beetles was due to conditions surrounding and incident upon the germinal materials in their most sensitive stages, before, during and immediately following fertilization. The behavior common to this type of experiment is shown in Plate III.

With this cross of an *L. signaticollis* ♀ × ♂ *L. diversa*, the determination of dominance and the ensuing type of behavior is clearly a function of the conditions incident upon the combining germ plasms. In the repetition of Exp. No. H 409/411, the experiment was varied so that in some cases it was the first laid eggs that gave the behavior of Exp. No. H 409, and in others, it was the last laid eggs, or those of the middle of the reproductive period—showing that the results are not “age results,” nor due to segregations, nor orthogenesis giving one kind of germ at the start, another at the middle, and others at the close of the reproductive period.

Crosses Between L. signaticollis and L. undecimlineata.

More interesting and complicated results were obtained in crosses between *L. signaticollis* and *L. undecimlineata*, where there are contrasting characters between both larvæ and adults, differences in the specific pattern as a whole, in specific spots and in the general body color. Reference to Figs. 1 and 2 will show essentially what these differences are, as far as pattern and spots are concerned. In body color of the larvæ the difference is between a white in *L. undecimlineata* and a bright chrome yellow in *L. signaticollis*.

L. undecimlineata ♀ × ♂ *L. signaticollis*.

Exp. No. H 700 A.

A virgin female of *L. undecimlineata*, from Ex. No. 722, g. III (AA) was crossed with a male *L. signaticollis* from Ex. No. 419, g. XIII (CAAC) under the following conditions:

FOOD : NORMAL — UNIFORM.

T.		R. H.	
Day Av.	± 95° F. 3.5°.	Day Av.	84 per cent. ± 8 per cent.
Night Av.	± 89° F. 4.8°.	Night Av.	100 per cent.

This mating gave larvæ in the F_1 generation which were of the female parent type, *i. e.*, white without tergal spots in the third stage, and from these emerged a single type of adults, all of the female parental type. These, when inbred, came true, giving individuals like themselves, and continued to breed true for six generations. No traces of sporadic variations of any kind in either adult or larva were found, nor was there in this strain any trace of the male parental type. In this cross, which I have repeated five times, the male type was as completely eliminated as if it had never existed. Plate IV. shows the behavior in the first and second hybrid generations.

Question as to this result might be raised on the grounds that it is a case of parthenogenesis and not a case of hybridization at all. As a matter of fact, parthenogenesis in *Lep-tinotarsa* is unknown, and although I have repeatedly endeavored to obtain parthenogenetically developed individuals, I have always signally failed. Virgin females of *L. undecimlineata* have been repeatedly subjected to chemical stimuli (*i. e.*, injected salts of Cu, Na, Li, Sr, Ba, Cu, Zn, etc.), and physical stimuli (*i. e.*, mechanical shocks, electric stimuli, etc.), which might be productive of parthenogenetic development, but thus far without any success whatever.

In a second series of experiments, an exact duplicate of the first, a female was allowed to develop eggs and deposit them, and these eggs uniformly failed to develop even to the earliest cleavage stages. No development and no fertilized eggs were found from this female until the eggs were fertilized by a male *L. signaticollis*, when development progressed in the regular manner and gave results identical with those of the first experiment.

L. undecimlineata ♀ × ♂ *L. signaticollis*.

Exp. No. H 700 A.

A virgin female of *L. undecimlineata*, from Exp. No. 722, g. III (AB), was crossed with a male *L. signaticollis*, from Exp. No. 419, g. XIII (CAAC), under the following conditions:

FOOD : NORMAL — UNIFORM.

T.			R. H.		
Day Av.	75° F.	± 2° .	Day Av.	80	per cent. ± 5 per cent.
Night Av.	70° F.	± 3.5°.		80-90	per cent. ± 5 per cent.

From this cross there came larvæ which in the F_1 generation were all of the female parental type, and from these emerged a single class of adults intermediate between the two parents, a mid type. These adults, very uniform in character, when inbred, gave in the F_2 generation abundant progeny. The larvæ of the F_2 generation were in the first stage all alike; in the second stage they were clearly divisible into two classes in the proportion of white 245: yellow 190; while in the third stage the yellow larvæ further divided into larvæ which were yellow with black spots on the back (YIS), and yellow without black spots on the back (Yls). The white larvæ similarly divided into two classes, white with black spots (WhS), and white without black spots (Whs). The census of larvæ in the third stage gave for Pair C:

Whs	WhS	YIS	Yls
170	75	58	132

Each of these classes of larvæ was somewhat variable, and it was often difficult to decide in the case of a white larva whether it belonged in the class with black spots or in the class without black spots, because there is an almost continuous gradation of color from zero to a full development of the dorsal color pattern. In making the division, the practice was followed of examining the larvæ with a lens magnifying ten diameters, and if the slightest trace of pigment was detected in the centres in which pigment develops, they were then classed as larvæ with spots, even though the spots were not visible to the unaided eye.

Each of these four classes of larvæ gave rise to three classes of adults, that is, each one split into forms like the female type, like the male type, and an intermediate type. In every case each of the four classes has given a typical Mendelian splitting in the second hybrid generation, but the ratios are in most cases somewhat variable, owing to the necessity of breeding these F_2 hybrids under rather variable conditions. The behavior in this culture is shown in Plate V. The census of the adults derived from Pair C was as follows:

	11- <i>lineata</i> type.	mid type.	sig. type.
170 Whs larvæ gave:	14♂ 22 ♀ 36	24♂ 25 ♀ 49	4♂ 7 ♀ 11
75 WhS larvæ gave:	3♂ 8 ♀ 11	9♂ 11 ♀ 20	6♂ 4 ♀ 10
58 YIS larvæ gave:	4♂ 4 ♀ 8	6♂ 10 ♀ 16	5♂ 4 ♀ 9
132 Yls larvæ gave:	9♂ 7 ♀ 16	22♂ 25 ♀ 27	17♂ 15 ♀ 32
Ratios of these adult types	71 :	132 :	62 :
Expected	63.75	127.50	63.75

Four experiments of this type have been carried through to the fourth and fifth generations with perfectly uniform results thus far.

L. undecimlineata ♀ × ♂ *L. signaticollis*.

Exp. No. H 701.

A virgin female of *L. undecimlineata*, from Exp. No. 722, g. IV (E), was crossed with a male *L. signaticollis*, from Exp. No. 419, g. XIII (CAAB) under the following conditions:

FOOD : NORMAL — UNIFORM.

T.	R. H.
Max. 105° F.	Max. 85 per cent.
Min. 80° F.	Min. 70 per cent.
Av. 92° F.	Av. 79 per cent.

The larvæ of the F_1 generation were in the first stage identical; in the second stage they were clearly divisible into sharply marked classes of white and yellow in the proportion of wh. 30:yl. 26. The yellow larvæ in the third stage divided into YIS 11 and Yls 9, and the white larvæ gave three groups: pure pearly white like the female parent, whs 1; larvæ which were yellowish white without spots, whys 14; and larvæ which were yellowish white with spots, whyS 10. The dorsal spots of the larvæ in the third stage were in this case variable. The single pearly white larva gave rise to a female exactly like the parent type and four classes of larvæ: white without spots (Whs), white with spots (WhS), yellow without spots (YIS), and yellow with spots (Yls). Each gave rise to a group of highly variable mid types, in which the range of variation was from the condition of the female parent to that of the male parent. Fourteen pairs of these were tested out in the F_2 generation and they were all found to be uniformly

mid types, that is, they were "heterozygous" in their nature and every one of them gave, when inbred, the following behavior in the F_2 generation: the larvæ in the first stage were all alike, in the second stage they were clearly divisible into two types, white and yellow in a proportion of approximately 1 : 1; in the third stage the larvæ of all the mid types divided into four classes: white without spots (Whs), white with spots (WhS), yellow without spots (YIS), and yellow with spots (YIs); and each of these classes gave three classes of adults, that is, from the white larvæ without spots came forms which were exactly like the female parent, forms exactly like the male parent, and an intermediate type. The same classes of adults came from the white larvæ without spots, from the white larvæ with spots, from the yellow larvæ with spots and the yellow larvæ without spots, giving thus twelve sharply marked categories of adults in the second hybrid generation, each having a definite type of behavior and carrying presumably a definite gametic constitution, the product of its past experience. The census of larval characters from nine matings was as follows:

	Whs.	WhS.	YIS.	YIs.	Total.
Pair A.	110	39	28	53	230
Pair B.	233	92	30	71	426
Pair C.	248	83	65	116	512
Pair D.	92	72	44	51	259
Pair E.	107	64	40	31	243
Pair G.	111	29	57	102	399
Pair I.	70	22	21	52	165
Pair K.	170	75	58	132	435
Pair L.	271	69	70	164	574
Total.	1,411	545	413	772	3,243

From these larvæ there came the three types: *signaticollis* (sig.), mid (mid), and *undecimlineata* (11-lin.) as follows:

	Whs. Larvæ.			WhS Larvæ.			YIS Larvæ.			YIs Larvæ.		
	11-lin.	mid.	sig.	11-lin.	mid.	sig.	11-lin.	mid.	sig.	11-lin.	mid.	sig.
Pair A.	15	34	14	5	14	6	2	8	10	7	21	12
Pair B.	39	43	20	13	35	5	3	10	5	6	28	9
Pair C.	43	72	32	20	26	9	10	27	19	7	26	12
Pair I.	14	36	7	4	8	6	1 ¹	8	7	1	28	13
Pair K.	36	49	11	11	20	10	4	16	9	16	47	32
Total.	147	234	84	53	103	36	20	69	50	37	150	78

¹A hybrid sport ♀ with the elytral stripes double — because the ancestor of a stable race.

OR

	11-lin.	mid.	sig.
Observed.	257 :	556 :	288.
Expected.	275 :	550.50 :	275 25.

These have been carried on into subsequent generations, and it has been found that the twelve extracted types resulting in the second hybrid generation are different from each other, even though they may appear superficially alike. The general behavior and results obtained in this experiment are shown in Plate VI.

L. undecimlineata ♀ × ♂ *L. signaticollis*.

Exp. No. H 700.

A virgin female of *L. undecimlineata*, from Exp. No. 722, g. I, was crossed with a male *L. signaticollis*, from Exp. No. 419, g. XI (DC), under the following conditions:

FOOD : NORMAL — UNIFORM.

T.	R. H.
Max. ± 81° F.	Max. ± 87 per cent.
Min. ± 70° F.	Min. ± 69 per cent.
Av. 75.6° F.	Av. 77.11 per cent.

This cross gave rise in the F_1 generation to larvæ all alike in the first stage, which in the second stage separated into two classes, yellow and white, and in the third stage remained as two classes, white without spote (Whs) and yellow without spots (Yls) (Whs 37 : Yls 45). The white larvæ (Whs) gave rise to twenty-one individuals exactly like the female type (12 ♂, 9 ♀), and the yellow without spots (Yls) gave rise to twenty-four individuals of the mid type (11 ♂ 13 ♀), a ratio of 7 : 8. The individuals like the female parental type, when inbred, gave a typical repetition of the ontogeny of the female parental stock with adults like themselves, and continued to do so for four consecutive generations without any indication of the male parent type appearing. The mid type, when inbred, gave in the F_2 generation typical results. The larvæ of the first stage were all alike; they divided into yellow and white larvæ in the second stage in the

proportion of yl. 83 : wh. 154, and in the third stage the white larvæ split into

Whs.	WhS.	YIS.	Yls.
38:	33:	31:	20.

or approximately 4 : 2 : 2 : 1. Each of these groups then gave rise to three classes of adults, precisely similar to those found to arise in the second hybrid generation in Exp. No. H 701, that is, from each of the four larval groups there arose forms like the female parent, others like the male parent, and an intermediate form; and these three categories of adults are clearly distinguishable one from the other without intermediates between them. The general results and behavior of this experiment are shown in Plate VII.

L. undecimlineata ♀ × ♂ *L. signaticollis*.

Exp. No. H 701 B.

A female *L. undecimlineata*, from Exp. No. 722, g. IV (E), and a male *L. signaticollis* from Exp. No. 419, g. XIII (CAAB), were crossed under the following conditions:

FOOD : NORMAL — UNIFORM.

T.	R. H.
Max. ± 98° F.	Max. ± 95 per cent.
Min. ± 59° F.	Min. ± 40 per cent.
Av. 80.2° F.	Av. 68 per cent.

and gave rise in the F_1 generation to larvæ which were all alike in the first stage, but which separated into yellow and white in the second stage, in a proportion of yl. 21 : wh. 28; the white larvæ remained white larvæ without spots in the third stage and the yellow larvæ remained yellow larvæ without spots in the third stage.

From the white larvæ without spots there came a type exactly like the female parent (2 ♂, 2 ♀), which, when inbred, continued to breed true; and from the yellow without spots came two classes of adults, a type exactly like the male parent (3 ♂, 2 ♀), and a mid type (3 ♂, 4 ♀); of the three types appearing in the F_1 generation, which are sharply marked one from another without any trace of intermediates, the observed numbers were:

11-lin. type.	mid type.	sig. type.
4 :	7 :	5.

In this experiment in the F_1 generation three distinct types appeared, one like the male parental type, one like the female parental type, and a mid type. Each of the derived types was inbred for four consecutive generations and continued to breed true, neither one giving any indication of the other stock. Of the mid types several pairs were mated and gave the same results as those obtained from the mid types in Exp. No. H 700, H 701, etc. Thus, in Pair A, the larvæ in the first stage were all alike; in the second stage they split into white and yellow in a ratio of wh. 55 : yl. 45. The white split into white without spots (Whs 27), and white with spots (WhS 23); and the yellow split into yellow without spots (Yls 14), and yellow with spots (YIS 25). The four classes of larvæ gave adults of the F_2 generation, each producing three classes sharply demarked one from the other, as in the previous experiments. Plate VIII. shows the behavior and results obtained in this experiment.

In this series of experiments the behavior in the first and second hybrid generations indicates a variability in the reactions which take place between the combinations brought about in the germ plasm at fertilization. As stated in the introduction, I have not been able to show the existence of additional characters latent or recessive, which might bring about the variability in behavior observed, and the problem is to account for this variability.

In the absence of evidence to the contrary, the characters seen may safely be assumed to represent the characters involved, and it is perfectly clear, in crosses between *L. signaticollis* and *L. diversa*, and between *L. signaticollis* and *L. undecimlineata*, that when identical materials were placed under dissimilar conditions, dissimilar types of behavior resulted without the production of anything new or unusual in the way of attributes in the resulting progeny. In the case of Exp. No. H 409, the behavior there strongly indicated that either one or the other of the two parents was heterozygous in character, and such an inter-

pretation would perhaps be perfectly valid were it not for the fact that identical materials placed under dissimilar conditions, as in Exp. No. H 410, give such a result that one would not be warranted in assuming that either of the parents was heterozygous, but that both parents were homozygous in the strictest sense. Even this might possibly be accounted for by assuming that chance had brought about the selection of homozygous individuals for one series of experiments and heterozygous individuals for the other. This interpretation, however, is invalidated by Exp. No. H 409/411, in which a male and a female of material identical with that used in Exp. No. 409 and Exp. No. 410 were allowed to reproduce under the conditions of Exp. No. 409 for part of their reproductive period, and under the conditions of Exp. No. 410 for the remainder. From the eggs developed and fertilized during the first period came results in every way comparable to those obtained in Exp. 409, and from the eggs developed and fertilized during the second period came results in every way the duplicate of those obtained in Exp. No. 410.

These experiments are crucial as far as this case is concerned, for the simple reason that it is inconceivable that during one period all the heterozygous germ cells would be developed, and during another period all the homozygous cells. Any such assumption is preposterous, and the only interpretation that one can legitimately use is that conditions surrounding and incident upon the germ cells at the time of and immediately following fertilization were in some way productive of the differences in behavior found.

In the series of experiments between *L. signaticollis* and *L. undecimlineata*, a more complicated behavior is found, due to the fact that more characters are involved. As in the first series, similar materials reared under dissimilar conditions gave dissimilar behaviors, but without the production of any new types or characters in the materials; that is, there are apparently no strange attributes present, but simply a variability in the behavior of attributes already present, and this variability in behavior may be of profound importance in evolutionary processes.

In this preliminary account of the experiments, I have given only the crosses between the female *L. signaticollis* and the males of *L. diversa* and the female *L. undecimlineata* and male *L. signaticollis*. The reciprocal crosses have been made and confirm in every way the results obtained in the crosses given, but in this paper the object is not the investigation of variability of behavior in reciprocal crosses, but an elementary consideration of the effect which incident or surrounding conditions may have upon the behavior of characters in hybridization. A more detailed treatment of this work must be postponed for a more extensive publication.

The results obtained in both sets of experiments are in general very much in harmony with results which have been obtained by certain workers in experimental embryology, with this difference, that in this case the analysis has been carried out through two or more generations, and in the case of experimental embryology the experiments cease with the obtaining of larval forms.

The whole question of dominance is at the present time a trying one. Practically all the criteria which have been proposed from time to time for the detection of the dominant member of a cross have in one way or another been broken down, and Davenport's definition, that the dominant member of a cross is only to be detected, in many organisms at least, by the determination of which character is the more variable in subsequent generations, seems to me not likely to be of general applicability. In the materials which form the basis of this paper it could not possibly be used, because both of the extracted forms are at times equally variable, at times one is more variable than the other, and at other times both are relatively invariable.

What determines the dominance of one parental type over the other is a question of vital importance in both normal and cross fertilization. Apparently, one of the earliest workers to attack this question was Vernon in 1898. He suggested that the hybrid echinoderm larvæ which in the summer were largely maternal in type, and in winter were largely paternal in type were due to the relative differences in the ripeness of the sexual products used in the cross.

Doncaster, in 1904, concluded that temperature was the chief,

if not the sole cause of the changes observed by Vernon; and Herbst's work in 1906-07 on the echinoderms showed definitely that temperature is a contributing, but not the exclusive factor. Tennent in 1910, by crossing *Hipponoë esculenta* with *Toxopneustes variegatus* at Dry Tortugas, Florida, reached the general result that in normal sea water *Hipponoë* is the dominant member of the cross in the *plutei*; and in sea water to which sodium hydrate had been added, increasing the alkalinity, he found that *Hipponoë* was also dominant irrespective of the direction of the cross; but when a small proportion of acetic or hydrochloric acid was added to normal sea water, thus decreasing the alkalinity, he found that *Toxopneustes* was dominant. This he considers an explanation of the seasonal variation described by Vernon, but it is not quite clear just what could be the basis of a seasonal variation of the alkalinity or acidity of a large body of ocean water like that of the Gulf of Mexico; rather, it is entirely conceivable, as Vernon states and as Herbst demonstrates, that temperature is at least a factor capable of producing variability in the dominance of various crosses. These results of Vernon, Doncaster, Herbst and Tennent deal with the early stages, and none have been carried to F_1 generation adults, or into the F_2 and F_3 generations. In my crosses exactly similar results have been produced by subjecting the organism to different sets of conditions during the fertilization period, and this has brought about divergence in behavior, which divergence has continued into the second and third generations, and the products of the variability are in every way constant and fixed from the start.

These results indicate that in the fertilization process the two somewhat unlike germinal substances that are being combined, and interact one upon the other in exactly the same way that two non-living substances would; that is, the products of the interaction are the resultant of the natures of the two substances and the conditions under which the combination took place. We must not, therefore, expect to find a factor which determines dominance, such as temperature, alkalinity, moisture, etc., but rather must determine the complex under which, when two materials are combined, definite

results are produced. When the same materials are combined under the conditions of some other complex we may expect, and do find, that there are differences in the behavior and in the products produced.

That this production of variability in behavior and in the determination of dominance by incident factors is a real and vital process in nature, I have attempted to show by a second series of experiments, in which I placed definite organisms together in a state of nature where they would interbreed freely, in order to see what the resulting products would be. These are the experiments in synthesis.

EXPERIMENTS IN SYNTHESIS.

The purpose of these experiments was to determine what the result would be when species which cross freely, and some of whose characters behave Mendelianwise in experiment, were brought together in a state of nature. It is frequently maintained, especially by systematists, that crossing in nature, while uncommon, when it does occur is without much effect—a broad statement made *à priori*, and grounded in the orthodox belief that species for the most part are physiologically isolated one from another.

An extensive set of these experiments has been in progress for some years, some few of which have now developed far enough to allow of rather definite statements. The method employed has been to take species derived from nature from some restricted locality, to keep close watch upon what goes on in this locality and also to analyze the composition of the species from this locality by cultures in the laboratory. In this way, stocks of known character are obtained from experiment, and also natural stocks whose attributes are well known are developed in the type localities. In the experiments in synthesis either pedigreed stocks from the laboratory, or the stocks from nature, or both, were placed in nature upon their food plant in isolated localities, or in large cages, and allowed to breed as if the introduction were a natural one.

COMPETITION HYBRIDIZATION EXPERIMENTS BETWEEN
L. signaticollis AND *L. undecimlineata*.

L. undecimlineata \times *L. signaticollis*.

Exp. No. C. H. 47.3 Cuernavaca.

In 1904, an isolated area of about an acre upon the southern slope of a barranca, near Cuernavaca, was planted with food plants, upon which both *L. signaticollis* and *L. undecimlineata* would feed. In July, 1904, this spot was stocked with a culture of 210 specimens of *L. signaticollis*, from a standard location about a mile and half distant, and 354 specimens of *L. undecimlineata*, obtained at El Hule, on the banks of the Rio Papaloapan. Each of the groups was equally divided between the sexes, were young and vigorous, immediately began breeding and intercrossed freely. Under experimental conditions these forms cross freely in both directions, but out of them no new characters come as the result of ordinary crossing.

In the first generation of this colony there was an abundance of individuals of both sexes of the *signaticollis* type, and of the *undecimlineata* type, and of a highly variable intermediate hybrid type. A census was made of the population on August 14 to 17, with the following results:

<i>signaticollis</i> type	mid type.	<i>undecimlineata</i> type.
4,518	11,744	5,091

In this experiment, it was, of course, impossible to tell from inspection whether the *signaticollis* individuals were pure *signaticollis*, or pure *signaticollis* and a hybrid with the *signaticollis* dominant, and the same was true with respect to the *undecimlineata*. All of the beetles entered into hibernation during the latter part of August, and early September of 1904. The food plants survived the long hard dry season and came up in the spring of 1905 in abundance, and in June, 1905, individuals of all three types emerged and were found to be interbreeding freely. A census made of the individual which emerged late in June gave the following results:

<i>signaticollis</i> type.	mid type.	<i>undecimlineata</i> type.
1,027	1,744	478

which clearly indicates that through some cause the hibernating conditions of the location were favorable for *signaticollis*, but were decidedly unfavorable for the *undecimlineata* and for the intermediate hybrid type. These individuals were allowed to interbreed freely and produced a numerous progeny, in which the larvæ were of four different types; white without spots, white with spots, yellow without spots, and yellow with spots. The second generation emerged from the middle to the end of July, 1905, and showed a huge preponderance of the *signaticollis* type. The census of a random sample taken the last week in July gave the following count:

<i>signaticollis</i> type.	mid type.	<i>undecimlineata</i> type.
1,244	1,192	367

These individuals were not removed from the colony; the census of the sample was made, the individuals put back, and the colony allowed to encounter the conditions and behavior which it would meet in a state of nature. Nine pairs, taken at random, of the *undecimlineata* type were bred out as pedigreed cultures during August and part of September, 1905, and gave uniformly an *undecimlineata* progeny. Seven pairs of the *signaticollis* type, which were bred out, gave uniformly a *signaticollis* progeny, and out of five other pairs there appeared individuals of the mid type and of the *undecimlineata* type, showing that some of the *signaticollis* type were hybrid in character. Six pairs of the mid type were also bred out as pedigreed stock, and showed themselves to be in every case hybrid.

The third generation was produced in August and early September, 1905. In this the larvæ were of the same four classes, but showed a huge preponderance of yellow larvæ (YIS). A count made late in August, when perhaps the bulk of the larvæ had entered into pupation, gave the following results:

Whs	WhS	YIS	Yls
205	227	849	321

The adults of Generation III. emerged early in September; a census made about the middle of September gave the following:

<i>signaticollis</i> type.	mid. type.	<i>undecimlineata</i> type.
2,452	827	218

showing again a marked decrease in the *undecimlineata* form, a lesser decrease in the intermediate hybrid type, and a much greater relative increase in the *signaticollis* type. These hibernated during the winter of 1905-1906 and emerged in June, 1906. They were allowed to interbreed freely. The population was not seen at the time of emergence, but in the fourth generation it was observed in July, 1906, and the 11-*lineata* type and the mid type were nearly absent. The census made at this time, when the first generation of the year was apparently at its height, gave the following results:

<i>signaticollis</i> type.	mid type.	<i>undecimlineata</i> type.
3,275	45	7

These then inbred and the colony was next seen in September at about the middle of the month, when the census of the individuals in the colony was as follows in Generation V.:

<i>signaticollis</i> type.	mid type.	<i>undecimlineata</i> type.
1,823	6	0

These hibernated during the winter of 1906-07 and emerged in June, 1907, reproduced at once, and gave an abundant progeny which emerged as Generation VI. between the 10th and 25th of July. These when seriated gave the following results:

<i>signaticollis</i> type.	mid type.	<i>undecimlineata</i> type.
2,255	2	0

The second generation of 1907 emerged late in August and early in September, and of this generation the *undecimlineata* type was entirely absent, and the mid type practically so. These hibernated and when seen in the spring of 1908 only the *signaticollis* type emerged. Both generations of 1908 and both generations of 1909 have developed the presence of the *signaticollis* type only.

In 1908 individuals from this location were brought to Chicago and carried as pedigreed cultures in the laboratory. They have shown a complete gametic purity as far as could be determined, and none have been detected which were hybrid in character. In this colony, isolated in its location, through some process or other in hybridization or perhaps by selective factors, *signaticollis* has completely subjected and eliminated *undecimlineata*. Inasmuch as *L. undecimlineata*, when protected from crossing, lives well at Cuernavaca, and the selective action is very low, I am of the opinion that the swamping of *undecimlineata* is due to some process of hybridization. This opinion is fully justified by experiments conducted in cages which eliminate selective factors.

L. undecimlineata \times *L. signaticollis*.

Exp. No. C. H. 47.4 Paraiso.

This experiment was begun in 1905, when one hundred individuals were taken from the standard colony of *L. signaticollis* at Cuernavaca, and, with an equal number of *L. undecimlineata*, from El Hule, were planted upon a vigorous growth of their food plants in a clearing made in the Foot Hill Rain Forest, in the Paraiso district not far from Ojos de Agua, in the Canton of Zongolica. They were observed to intercross freely, but there was a preponderance of *undecimlineata*-like forms, with a few intermediates, and only small numbers of the *signaticollis* type in the first hybrid generation. The census made of the first hybrid generation was as follows:

<i>signaticollis</i> type.	mid type.	<i>undecimlineata</i> type.
0	56	1,342

A third generation was produced in late November, and in that generation there were no *signaticollis* forms visible; there were only a few of the hybrid intermediate type and these all closely approximated the *undecimlineata* form. The census obtained late in November was

<i>signaticollis</i> type.	mid type.	<i>undecimlineata</i> type.
0	11	1,134

In 1906, 1907 and 1908 these cultures were allowed to shift for themselves, and the food plants were nearly swamped by immigration into the glade of plants from the surrounding Rain Forest; in fact, the whole culture was allowed to engage in a most desperate struggle for its existence. As far as the beetles were concerned, this was simply a struggle for food. In 1908-1909 the inroads which had been made by other plants had so reduced the number of *Solanums* that the food supply was inadequate. During these years, however, no trace of the *signaticollis* type has ever appeared. In 1908, material of the *undecimlineata* type was taken from this culture to Chicago, and there subjected to the tests of pedigree analysis, but without any trace of the *signaticollis* form appearing. In both experiments, however, at Præsidio and at Cuernavaca, the resulting materials were different in the gametic make-up from the original species. Superficially, these stocks could not be told from the natural species, but when used as the basis of experiment under control conditions, it was found that there resulted a difference in the behavior of the subsequent hybrid generations, clearly indicating a change in the gametic constitution of these groups of individuals.

Other experiments involving the same two species are in progress, under desert conditions at Tucson, Ariz.

Competition Hybridization Experiments Between L. decemlineata, L. oblongata and L. multitæniata.

A series of experiments, more conclusive and under better conditions, has been carried on, using three species: *L. decemlineata*, *L. oblongata* and *L. multitæniata*. Of these, in nature, *L. decemlineata* is limited solely to the United States and southern Canada; *L. multitæniata* entirely to the southern portion of the plateau of Mexico, and *L. oblongata* to the Balsas Valley and the Oaxaca-Guerrero Highlands. These species inter-cross freely under experimental conditions and present the following contrasting characters for consideration. The general ground color of the larvæ of *L. decemlineata* is wine red, that of *L. oblongata* and *L. multitæniata* chrome yellow. *L. decemlineata* and *L. multitæniata* have two rows of spots along the side in the larvæ,

while *L. oblongata* has one. *L. oblongata*, as shown in Fig. 4, is long and oval in outline; *L. decemlineata*, as shown in Fig. 4, is more rounded; and *L. multitanziata* is robust in type. There are also color differences between the species, which need not concern us here. Three experiments will serve to illustrate the purpose of this paper.

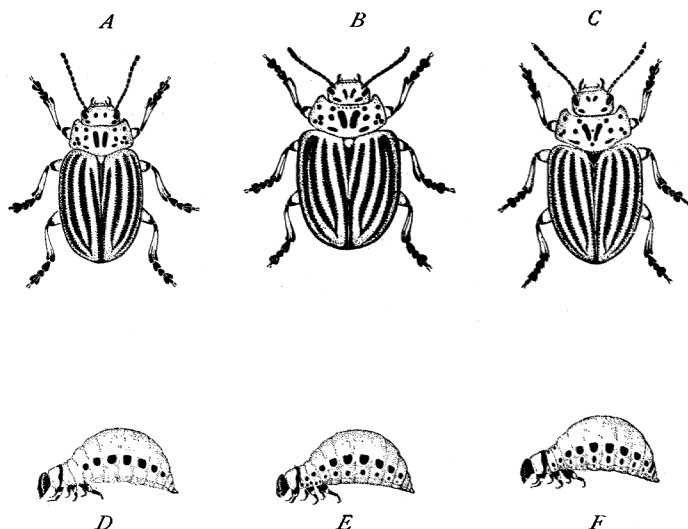


FIG. 4. Arranged to show some of the essential differences between the species; *L. oblongata*, *L. multitanziata* and *L. decemlineata*. (A) Showing the form and characteristic markings of the adult of *L. oblongata*. (B) Adult of *L. multitanziata*, showing the more robust form and somewhat different type of general color pattern, sharply distinguishing it from both of the other species. The elytral ground color is often dark ochre, sometimes even reddish. (C) The type of *L. decemlineata* used in these experiments, somewhat intermediate between the two other species in body form, and to a certain extent in markings. (D) Showing the side view of a full grown larva, with its color pattern. The ground color is yellow and that of the adult somewhat variable. (E) Adult larva of *L. multitanziata*, with the characteristic color pattern. Ground color is yellow as in *L. oblongata*, but darker. (F) Shows the characteristic color pattern of *L. decemlineata*; the ground color of the larvæ is wine red.

L. decimlineata \times *L. oblongata* \times *multitanziata*.

Exp. No. C. H. 156.2 Balsas.

In 1905, twenty *L. decemlineata*, from pedigreed culture Ex. No. 99, g. X from Chicago; twenty *L. oblongata*, from pedigreed culture at Cuernavaca, and twenty *L. multitanziata*, derived from

an isolated standard locality in the valley of Mexico south of Guadalupe, were placed on an isolated island in the Balsas River. This island was fairly well covered with a growth of *Solanum rostratum*, or a closely related form, upon which all three species would feed. As far as could be discovered, the island was devoid of any individuals of *L. oblongata* which occur very sparingly in that general region, and the neighboring banks of the river and the islands were all searched, but they afforded no trace of *L. oblongata*. These introduced beetles were allowed to breed and gave the first hybrid generation in August, 1905. In this generation only the adults were seen, and of the adults we could recognize definitely five forms:

(A) Those which on inspection appeared to be wholly *L. decemlineata*; (B) those which appeared to be wholly *L. oblongata*; and (C) those which appeared to be wholly *L. multiteniata*. There were individuals which were manifestly intermediate hybrids, in form, punctuation and coloration, between *L. decemlineata* and *L. oblongata* (D); and between *L. decemlineata* and *L. multiteniata* (E). Of these five forms a census was made with the following results:

A	B	C	D	E
327	371	142	1,439	246

All the individuals were allowed to remain in the colony and interbred freely in August, giving early in September a second generation, of which the following census was made:

A	B	C	D	E
46	101	90	1,292	210

These hibernated during the winter of 1905-1906, and were not seen again until September, 1906, in the fourth hybrid generation of the culture. At this time the dominant form was manifestly a combination between *L. decemlineata*, *L. oblongata* and *L. multiteniata*, with the *oblongata-decemlineata* attributes in excess of those of *L. multiteniata*. (A combination between classes D and E of F₁ and F₂.)

A	B	C	D + E
7	25	12	2,210

The huge preponderance of this complex type, which was neither one nor the other of the three species, suggests at once, of course, that the results could not be due to any selective process, because the type was not one of the original types but a hybrid complex which was preserved because of its fitness for the location in which it was living.

The wintering condition of 1906-1907 were especially rigorous, at least as judged by the number of beetles that I found in that location in 1906-07, when the following census was made:

A	B	C	D + E
0	0	4	422

This shows that during the winter practically only the hybrid combination was able to survive. These reproduced and gave a progeny late in July, 1907. An inspection was made early in August when I found only the dominant type present in the fifth hybrid generation.

A	B	C	D + E
0	0	0	1,877

The culture was not seen again until the spring of 1908, when a considerable number of the dominant form of the sixth hybrid generation was found emerging. These were taken to Chicago and subjected to analytical experiments and were found to breed true, both in group and in pedigreed cultures, with this exception, that in both group and pedigreed cultures, there occurred from time to time sporadic variants often standing a considerable distance apart from the rest of the population, which, when inbred, either with sports like themselves, or back to the parent type, gave behaviors which in every way are comparable to the behavior observed in many of the forms which are supposed to have arisen by a mutative process. These strains were kept through the years 1908 and 1909, and gave results which strongly suggested that the interpretation of a mutative period, as de-

scribed by De Vries in *Oenothera Lamarckiana*, may well be the variability which follows complex processes of hybridization.

L. decemlineata \times *L. oblongata* \times *L. multitaeniata*.

Exp. No. C. H. 156.4 Escamela.

In 1906 operations were begun at Orizaba, and in May the same three species from the same original stocks were mated. Conditions at Orizaba are decidedly different from those in the Balsas Valley. The city is 2,000 feet higher in altitude and the climate is very different. In the Balsas Valley during the summer the days are bright and hot, with evening showers. At Orizaba, in the location chosen at the foot of the Sierra Escamela, it is never above 90° even on the hottest days, and the nights are always cool, owing to the downward draught of cool air from the mountains which flows over the valley at night. The relative humidity is high at all times, and the precipitation during the season was 74 inches.

Under these conditions the crosses which were made thrived as far as certain members were concerned; the *L. multitaeniata* individuals were decidedly reduced by the conditions under which they were living and the *L. oblongata* individuals were hampered considerably, but to a lesser degree. Crossing was observed, however, among the component species in all directions, and progeny emerged in July, showing a combination to have been formed between *L. oblongata* and *L. decemlineata*, with the *L. multitaeniata* type and attributes practically wanting. The population, when examined, showed individuals which were apparently dominated by *L. decemlineata* (A) to the exclusion (as far as visible) of all others; individuals which were very clearly intermediate between *L. decemlineata* and *L. oblongata* (B); and individuals which were more or less intermediate between *L. decemlineata* and *L. multitaeniata* (C). Of these the intermediate between *L. decemlineata* and *L. oblongata* existed in by far the greatest numbers, as shown by the following proportion:

A	B	C
131	397	92

In as much as this experiment was conducted in a large cage and not in the open, it was manifestly impossible to utilize all the individuals which emerged, so a reduction was made for the matings for F_2 , excepting that any extreme or rare types were given every advantage over the more common types. The following materials were selected at random from the different groups as parents of the second generation:

A	B	C
3♂ 3♀	3♂ 3♀	3♂ 3♀

These inbred rapidly during July and at the end of August gave a second generation which was uniformly an intermediate between *L. decemlineata* and *L. oblongata*.

A	B	C
0	589	0

This was especially true of the adult characters. The larval characters, however, were also variable and appeared to be less blended into a homogeneous group.

The culture hibernated from early September, 1906, to June, 1907. During this period a very great mortality occurred, which was due very largely, I think, to the fact that the culture would probably have reproduced a third time in 1906 if it had been supplied with food and proper conditions.

These individuals in 1907 reproduced and gave a pretty uniform progeny of the blended type between *L. decemlineata* and *L. oblongata*, generation III.

A	B	C
2	476	0

A fourth generation was obtained in late August and early September of the same year, which possessed the same attributes as the third generation. In nature, this culture was not carried beyond that stage, but material from the culture was brought to Chicago and carried through the winters of 1907 and 1908,

and the summer of 1908 and part of 1909. It was subjected to various analytical experiments, all of which tended to show that the type was a relatively stable one. Individual pairs, when inbred, gave a very definite pure line culture, and groups mated at random gave the same result; but, as in the colony in the Balsas River, there appeared sporadic individuals, widely separated from the parent stock, which, when inbred, behaved very much as mutants are supposed to do.

L. decemlineata \times *L. oblongata* \times *L. multitæniata*.

Exp. No. C. H. 156.8 Tucson.

A culture of the same material was placed at the Desert Botanical Laboratory of the Carnegie Institution in the desert of Southern Arizona at Tucson near the foot of Tumamoc Hill. In this experiment two males and two females of *L. decemlineata*, from Exp. No. 99, g. XIII, from typical stock at Chicago, two males and two females of *L. oblongata* from Exp. No. 619, g. XI, and two males and two females of *L. multitæniata*, from Exp. No. 543, G. XI, were mated in the early part of June. This culture was confined in a cage six feet square on the ground and three feet high, covered with wire eighteen meshes to the inch, thus eliminating all selection by insectivorous enemies. *Solanum rostratum* was supplied as food in sufficient quantity. During June and July these reproduced abundantly and gave a large progeny which emerged late in July and early in August. In this first hybrid generation at Tucson there was, as in the other cultures, a blending of the materials introduced into the experiment, but in this culture *L. decemlineata* was the dominant member of the cross, although not completely.

In the larvæ six types were observed:

1. Those which on inspection appeared to be *L. decemlineata*.
2. Those which were *L. oblongata*.
3. Those which were *L. multitæniata*.
4. Those which were intermediate between *L. decemlineata* and *L. multitæniata*.
5. Those which were intermediate between *L. decemlineata* and *L. oblongata*.
6. Those intermediate between *L. oblongata* and *L. multitæniata*.

It was, of course, impossible to tell on inspection what the constitution of each of these types was.

Five classes of adults were recognized:

- (a) Those which were clearly either pure, or dominants of the *L. oblongata* type.
- (b) Those which were clearly intermediate hybrids between *L. decemlineata* and *L. oblongata*.
- (c) An *L. decemlineata* type in which *L. decemlineata* was in the main dominant, but which exhibited a variable range of variability.
- (d) Intermediate hybrids between *L. decemlineata* and *L. multitæniata*.
- (e) Forms which were either *L. multitæniata* pure, or heterozygotes in which *L. multitæniata* was completely dominant.

Out of 1,857 adults seriated, the following census was made:

A	B	C	D	E
47	29	1,311	261	103

This census shows that while *L. decemlineata* is either the dominant or prepotent member of the combination, it did not come out of the mixture entirely without contamination.

This experiment was continued in a cage exactly like the first, and the following materials were taken at random from the first generation as the parents of Generation II.

A	B	C	D	E
2 ♂	2 ♂	6 ♂	3 ♂	3 ♂
2 ♀	2 ♀	6 ♀	3 ♀	3 ♀

This material immediately began breeding and gave during the month of August a large progeny which emerged early in September, and immediately went into hibernation. When seriated, this material gave the following results:

A	B	C	D	E
0	29	247	42	0

These passed the winter of 1908-09 in the ground and emerged in June, 1909. All that emerged were allowed to reproduce in

the cage and were supplied with food as fast as it was consumed. These gave a very large progeny which appeared to be uniformly of the dominant types of the first and second generations. Seriation of the material obtained from Generation III. at the end of August, 1909, gave the following results:

A	B	C	D	E
0	5	362	8	0

I then mated at random for the parents of Generation IV., one male of B, the only one that could be found alive, three males and three females of C, two males and two females of D, and none of E, they being absent. This material bred at once and gave in the fourth generation a considerable progeny, which were all of the dominant type.

Material from Generation IV., brought to Chicago in August, 1909, placed in hibernation under experimental conditions and brought out to breed in the middle of the winter, has shown that the dominant type is a fixed type, and that it breeds true and does not split in subsequent generations. The only splitting is that which occurs in rare individuals in from two to three per cent. of the progeny, which stand apart from the general population as sports. These cases are practically the reappearance of one or the other of the component characters or combinations thereof that went into the cross, and they do not represent in this experiment anything in the way of characters new to the genus or family, as DeVries states to be true of his mutants; rather, they are simply the characters obtained from the different parents from which this complex has been built up.

The same combination of material was made in Chicago in 1908, and was run through essentially the same procedure as that of the Tucson experiment, with this difference in the result, that at Chicago *L. decemlineata* completely dominated the culture to the total exclusion, as far as analysis has been able to discover, of the presence of the other parents.

These experiments in synthesis represent what might happen in a state of nature when species which can hybridize migrate from one place to another and intercross. No one realizes

better than I the complexity of experiments of this kind, the difficulties involved in the analysis of the results, and the caution that should be exercised in making statements from them. It seems certain from these experiments, as far as they have been carried out, and they are by no means complete, that we may definitely conclude that when like materials are combined under different natural environments, differences in the products, depending upon the conditions under which the combination take place, result. It is certain that the type which came out of the culture in the Balsas Valley was quite different from that which resulted from the cultures at Orizaba, and these are different from the dominant type which arose at Tucson.

Whether or not the dominant types resulting in these experiments differ sufficiently to be called species is a matter of opinion. To judge by analogy, I suspect that if a systematist had found these materials in nature they would have been classed as species, or at least would have been given the value of a variety. Since their history is known, I presume that they lose all claim to any specific or varietal distinction, from a systematic standpoint. The experiments, however, clearly indicate that the process of hybridization carried out under divergent conditions in nature gives identical results, as far as principle is concerned, with the crosses carried out under divergent conditions in experiment. It is true that these cultures are group cultures and are synthetic and not analytic, but a series of experiments is being conducted under diverse natural environments, which gives promise of confirming the general point, that conditions incident or external to the germ cell at the time of fertilization may profoundly modify the behavior and the relationships of the characters entering into the crosses.

One point of very considerable interest is the behavior of these dominant types in exactly the way in which DeVries's *Oenothera Lamarckiana* behaves, giving in each generation a greater or less number of rather divergent individuals, which, when inbred, are found to be stable germinal variations. I shall report upon this more extensively in another paper.

Bateson (1902, p. 153) has suggested that the mutations observed by DeVries in *Oenothera Lamarckiana* are in reality due to some

sort of hybridization behavior. I am of the opinion that Bateson's suspicion is probably justified, at least in some instances. I have no experience with plants and especially none with *Ænothera Lamarckiana*, but my experience with these synthetic experiments has suggested that the type of behavior which DeVries has discovered, and upon which he has built an all-inclusive theory of evolution, is in reality nothing more than the reappearance from time to time of attributes brought into a strain by hybridization, and which reappear in every generation, or in frequent generations, by some process akin to Mendelian segregation.

It seems unreasonable to advance, as has DeVries, the idea of a pre-mutation period, with a gradual development of invisible pangenes, and then a final bursting of these pangenes into a full-fledged mutation period, followed by a gradual dying away of the mutation period which leaves a species in a condition in which it does not produce these sports. Rather, the explanation which Bateson suggested, and which I have shown to be capable of creation in these synthetic experiments, is far more plausible and more likely to be the real explanation of the type of behavior found.

This raises a very large question—one that has been raised many times—as to whether natural species may not be hybridization complexes rather than pure line cultures isolated by some sort of selection, as has been presupposed since the time of Darwin. I have found that in nature, crossing, especially between these chrysomelid beetles, is by no means uncommon, and very frequently results in adult progeny in nature, some of which have been described as species. These natural cases of hybridization have been observed in the last half dozen years along the edge of the Mexican plateau. Some other species of chrysomelids from the same general region, especially some species of *Labidomera*, have a variability strongly suggestive of a similar origin. I have found that *Labidomera suturella* Chevr., of which many sharply marked variations have been described, gives a variability in pedigreed cultures that is strongly suggestive of the species having arisen through a process of hybridization. On the high volcanic plateau of Toluca there is another type

rather closely allied to *L. multitæniata*, which is also suggestive of having arisen, or of being in the process of arising, through hybridization.

These conditions in nature are of course difficult or impossible to check and verify, because the past is absolutely unknown, and little or no indication of what it has been can be obtained from any source. The materials in museums and the records by systematists are utterly useless for this purpose. Apparently, the only way of attacking this problem is the one which I have adopted of placing colonies in isolated locations, or in cages, there to carry out the process of interbreeding and forming of hybrid combinations as would occur in nature.

DISCUSSION.

Neo-Mendelism, The Factorial Hypothesis, and Theories of Germ-Plasm Composition.

The essence of Neo-Mendelism is based upon the actual experimental evidence of many workers, and is the idea that such of the attributes of organisms as show this type of behavior are the product of two factors which come into the fertilized egg, one from each parent, and that in gametogenesis these factors are distributed among the gametes by some process which is symbolized as "segregation." This factorial point of view is in no wise, of necessity, to be tied to or confounded with such speculations as the id-determinant-biophore fabric of Weismann, nor with the pangene complex of DeVries, which have no foundation in fact.

I doubt very much if Davenport (1910) will find many Neo-Mendelians willing to subscribe to his statement—"In studying heredity our attention must often be focused on the ontogenesis of the different characters, and we are sometimes inclined to regard the adult character as the product of the course of ontogenesis. But this is a superficial way of looking at things; the determiners of all characters are in the germ-plasm and together they direct the development of one part after another in orderly succession; a modernized form of the preformation doctrine seems logically necessary." That the determiners of all charac-

ters are in the germ-plasm is something we do not know, and to say that together they direct the development of one part after another in orderly succession puts upon these determiners a burden of great responsibility, almost of intelligence, and makes necessary some coordinating mechanism behind it all.

What we do know is that in some way, as yet unknown, in the germ-plasm there is conditioned the basis upon which the attributes of the future organism are to be built. It is a fact of experience that the germ cells give, on being combined at fertilization, results which suggest that the germ cells are of unlike potentiality or constitution with respect to a given character, and this is further strengthened by experiments wherein the results are exactly predicable when the germinal constitution is known. What this difference in the gametes is, we do not know, but observed behaviors are interpreted as being, most probably, due to the mechanical separation into different germ cells of whatever is it that produces the contrasting attributes—segregation during gametogenesis.

There is, furthermore, a very considerable amount of evidence, aside from that obtained by Neo-Mendelians, to substantiate this factorial point of view. The Mendelian behavior is most commonly found in color and color characters, and in color characters two definite general processes are involved; first, the production of the pigment to produce color; and second, the localization of this pigment in definite positions in the organism. The color itself is known very definitely to be, in a large number of cases, if not generally, the result of the interaction of two chemical substances. Riddle (1909) brings together from diverse sources the knowledge available concerning the formation of the melanin pigments, and, as far as known, the production of these pigments is uniformly due to the existence of an oxidizing agent—tyrosinase—and a substance which is oxidizable—tyrosin or allied compounds. In the test-tube of the physiological chemist, the tyrosin will remain tyrosin indefinitely unless it be oxidized by the tyrosinase into some simpler substances, when the color-forming compound appears, and exactly the same is true in the living organism. Also the tyrosinase will indefinitely remain tyrosinase, without the formation of color, unless

tyrosin be present. There is in this production of melanin pigment exactly the requirements of the Neo-Mendelian factorial hypothesis, as suggested by Cuènot (1903) and developed by many workers in the last few years—two things which must be brought together to produce a definite end result, or if one be absent then the one present is incapable of producing the customary result, *i. e.*, pigment.

In plants, it has been shown by Correns, by Bateson and his students, and others, that two factors are necessary to produce color; and in *Antirrhinum*, Wheldale (1907) and Wheldale, Maryat and Sollar (1909) have a considerable body of evidence to show that there are specific chemical substances—chromogens—to be oxidized to produce the colors of the flowers. Bateson (1909) has clearly stated that this does not mean that any substance, as a specific substance, or entity, is segregated in the germ cells; it simply means that a capacity for the production of either one or the other, or both of them, must be present in order to produce definite results. This capacity, as far as my experience goes, seems in all cases to be a property of the whole organism, which during ontogeny, manifests itself epigenetically, now in one part or character, now in another, and a very simple change at the start may conceivably result in extensive end results. I am, while fully convinced of the truth of the behavior of characters Mendelianwise, equally unconvinced, as the result of ample experience, that the process is in any way due to a particulate composition of the germ-plasm, or to any sort of preformation, and as far as I am aware, no Neo-Mendelian has thus far attempted to form any conception of what it is in the germ cells that is productive of the observed results, and only rarely do we find such concrete statements of preformation as that made by Davenport.

Castle (1909, page 68) expresses more accurately the current Neo-Mendelian conception of these factors: "In what form, it may be asked, are we to suppose that the various assumed factors exist. Do they occur as so many different substances lying side by side but unmixed in every reproductive cell? . . .

"It is, we think, not necessary to suppose that there exist in the minute germ-cell as many complex organic substances as

there are activities of the cell; neither is it necessary to suppose a different substance present for every independent factor identified. The various independent factors may have a basis no more complicated than that of so many atoms attached to a complex molecular structure. Experiment shows that the factors may be detached one by one from the organic complex. The discontinuity of their coming and going is entirely in harmony with the conception of them as components merely of complex molecular bodies."

If I understand Castle correctly, the atoms or groups thereof that are detached, are not of themselves the repository of capacities such that anywhere they would produce a given result, but rather, because of their absence in the complex group, the development of a character fails, and their presence is necessary to the appearance of the character in question. This conception is fundamentally different from the representative particle ideas of DeVries or Weismann, although the two ideas are not infrequently confused.

In the introduction (p. 1) I pointed out that the fundamental question which must be answered before we can get any real explanation of Mendelian behavior is, whether these "unit characters," are lesser entities conditioned by representative particles capable of mosaic rearrangement in the organism. It was further pointed out that to conceive of an organism as an entity analogous to a crystal, or as a mosaic more or less analogous in certain respects to granite or to orthoclase-feldspar crystals, expresses figuratively some of our experiences concerning the nature and composition of organisms.

There is, unquestionably, in all organic forms that which has the stability of form characteristic of crystals, and there is that which can be removed or replaced without in any way changing the basic form, exactly as impurities can be removed from or substituted for in crystals. Likewise, there are alternative conditions of existence of this basic form, which, like allotropic crystals, can exist only as one or the other form.

In germ cells the colloidal ground substance, which Lillie (1906, 1909) finds is not disturbed in its polarity and in its future developmental processes by powerful centrifugal force, may very

probably represent the more crystalline-like germinal basis, and any of the included granular substances or chromosomes which are capable of more or less alternation in relation and position, may conceivably in some way be connected with and indicative of the more superficial, removable, or changeable attributes.

The evidence derived from studies of accessory chromosomes and their segregation into germ cells during maturation, giving germs of different chromosomal constitution, is indicative of some difference in germinal composition. Whether these behaviors of chromosomes are the consequence of more fundamental germinal differences, or the initiation of subsequent germinal differences, is a problem for the future to decide. It does not of necessity follow that the chromosome is particulate, or the determiner of anything; it is at present an indicator of germinal difference which is coupled with whatever it is that determines the alternative nature of sex. If differences of this sort exist in one alternative character, there is no *à priori* reason why there may not be similar differences in others.

Our present experience indicates a germ plasm composition analogous to that of an orthoclase crystal, with a basis to which are added to or subtracted from through the reproductive process, attributes which become parts and properties of the whole. That the germ-plasm is such immortal material, irreversible in its action, that it possesses a oneness of constitution and ultimate destiny, is a conception based upon *à priori* dogmatic metaphysical concepts, and is a negation of the evidence of our senses.

Many years of experience with the problems of variation, heredity, and evolution, wherein germ-plasm constitution must play a vital part, have forced me to the formation of a conception of germinal substance like that expressed above. It is distinctly neither one nor the other of the older conceptions, but rather a mid-position, recognizing the elements of truth in both of the older conceptions, and is in entire harmony with the facts of experience. A presentation of my data and more extended elaboration of this conception cannot be attempted in this preliminary paper.

There is in this conception no element not in harmony with the existence of Mendelian behavior of characters, nor incom-

patible with a behavior in gametogenesis that would result in mechanical separation into unlike masses of germinal substance. No idea is expressed or implied in this conception of the nature of the physical state which conditions anything in the germ plasm, nor must the fact be lost sight of that this is a proximate conception of germinal substance and not an ultimate. At present in biology we have no business with ultimate conceptions, and the two thus far attempted of germinal constitution—the “particulate conception” and the “crystalline entity” are both equally dismal failures and equally useless as working hypotheses.

The conception herein set forward recognizes the following facts as regards organic constitution:

1. That there is in organisms a form basis, relatively unalterable as regards symmetry, pattern and arrangement of parts.

8. That there are in organisms an array of attributes capable of variation, but blending in heredity, forming blends and intermediates.

3. That there are in organisms an array of attributes which can exist only in a definite state of stability—they are either there or not there.

4. That there are in organisms characters that by crossing can be replaced by other more or less similar but different characters.

These four classes of attributes in some manner are conditioned by physical forces in the germ-plasm, and are, as far as we can perceive, the product of the past interactions between the germinal substances of past generations, and between these substances and the conditions of their existence and activity. Two chief series of physical events are at work; the series of events characteristic of any germinal substance—the product of its past history, the genetic forces—and the interaction of this substance with new germinal substances under the dynamic action of surrounding or incident forces. It follows from this that any germ cell is an epigenetic product of the two series of events necessary to the production of fertilized eggs and the resultant soma-germ complex, and the subsequent germinal changes may be large or small, in one or many of an unknown number of possible directions of modification; and while consequent somatic or germinal attributes may to us appear as either continuous or discon-

tinuous in results, in the interaction between the genetic state and the dynamic forces only continuity of process is probable on the basis of present physical knowledge.

This genetical-dynamic-hypothesis of germ-plasm constitution and modifiability, forms a convenient basis of departure for a host of evolution problems, and it is from such a theoretical basis that I have sought to study certain phases of the Mendelian phenomena.

Dominance.

The subject of dominance and recessiveness is at present decidedly an open question. What do we mean by dominance, and what is it that determines dominance? In the simpler cases, as illustrated by Mendel's peas and many others, there is no difficulty in stating positively which one of the two characters entering into a cross is the dominant member. Such examples are fairly abundant; they behave with considerable uniformity and represent a type of behavior for which there is some definite cause. What is it that makes one character recessive to the other? The Neo-Mendelian explanation is that one character is recessive and the other dominant because the recessive character is the absence of that which goes to make the dominant character. This explanation, however, while it may fit some characters, melanin pigment, for example, could not by any means fit all cases.

Thus, for example, in the experiments given in this paper, in crossing black stripes and no stripes, we may well conceive of the black stripes as being due to the presence of the two factors which produce black, and of no stripes as being due to the fact that one or both of the producing factors is absent. As far as the causation of color is concerned, this is actually the case, because I showed in 1903 that the black and brown color in these beetles is due to a substance in the cuticula which must be oxidized by an enzyme to produce the dark pigments. This is a clear example of the dominance of the presence over the absence, in some of the experiments and not in others. But the case is different in such crosses from that between tall and short stature in pea plants, tailed and rumpless condition in poultry, etc.; these must in one way or another be due to some sort of activity within the

organism. According to the theory of inhibitors, angora forms have long hair because the inhibitor of hair growth fails to act in one case, giving long hair, and acts in another, giving short hair; and poultry have tails because the inhibitor of tails fails to act in most cases, but acts rarely to give tailless birds, that is, the tail in birds is recessive to no tail, etc. This seems an extreme and unnecessary complication of the present hypothesis.

Unquestionably, something determines dominance in color, in tall and short peas, etc. Probably the most extreme cases of dominance are those which breed true without segregation in F_1 and subsequent generations. A behavior of this type is given in Exp. No. H 410, where the F_1 hybrid was exactly like the female parent and continued to breed true during the succeeding generations.

In Exp. No. H 409/411, there again appeared a dominant type, dominant to the complete exclusion of the other parent, which continued to breed true generation after generation; yet from the same parents there arose individuals which gave a different behavior, and both behaviors were based as far as any evidence is available, upon one and the same kind of germ cells. These cases represent dominance of the extreme kind, in which there is a total disappearance of the characters of one of the parents in the subsequent progeny. From these, we pass over such cases as those observed by Mendel and many others, to these F_1 hybrids in which the individuals are a blend and intermediate between the two parents. Such are given in several of the experiments cited in the body of this paper, and in some there were a series of gradations from the extreme of total dominance to the other extreme of an intermediate or blending condition between the two attributes.

In these blends, which are typical heterozygotes, the dominant attribute is diminished in manifestation in F_1 but appears undiminished in F_2 —but what shall we say of Exp. No. H 701 B, where in F_1 there appeared the *undecimlineata* type, mid type, and *signaticollis* type? In this series, from the same parents, the presence dominates the absence, blends therewith, is recessive thereto, in F_1 and only the mid types are heterozygous—all from one and the same pair of parents in each repetition of the experiment.

The question is, to what is this behavior and its variability due? The older writers confused dominance with prepotence, and the behavior was attributed to "strength," to the age of the parents at the time they reproduced, etc. As far as I can discover, the evidence for strength or age is anecdotal or very questionable in character, and in a long series of experiments I have been unable to get any evidence that age of the gametes or parents signifies anything in hybrid behaviors. Whatever is meant by strength no one can say, and to attribute behavior which gives dominance and recessiveness to differences in strength is meaningless. If by this "strength of germs" is meant energy for growth and development, we must, in order to utilize any such conception, know how much potential energy is stored in each germ—what the kinetic output would be when two germs were combined, and the increase or decrease of the kinetic output by conditions surrounding or incident upon the energy of the zygote. In other words, the friction of the developmental processes will vary and be as productive of resultant differences as are initial differences in the endowment of potential germinal energy, if such there be. Much more knowledge of germ-plasm physiology and dynamics is necessary before germinal energy can play any part in the explanation of hereditary behavior.

It has not thus far been shown that staleness of the germ cells is productive of any of the results which have been described. We know that germ cells become stale and that fertilization becomes difficult or impossible, and since development is slow or incomplete from stale germs it is possible that when germ cells that are stale are combined with those that are not, one or the other may dominate in the cross. I have attempted many experiments along this line, but thus far without any concrete evidence that staleness in itself is productive of any result.

In the present series of experiments there were involved in the elytral stripes of one parent:

1. Capacity to produce a substance capable of being oxidized to form colored compounds.

2. Capacity to produce an enzyme capable of oxidizing this substance.

In the other parent:

3. No capacity to produce either one or the other of the above.

The chief variables in these experiments were the conditions surrounding and incident upon the germ cells at the time of fertilization. All of the crosses herein recorded were made between individuals of the same age and always between vigorous individuals of their respective population; that is, the materials for crossing were always homogeneous as far as could possibly be determined, and I never mated an old male with a young female, or vice versa.

In these experiments I have succeeded in creating a series of behaviors in which the same characters are dominant to the complete exclusion of the others; dominant to a lesser degree, or in which there is a complete blend between the two in the F_1 generation, or the appearance of both parental types in F_1 and both breed true. As far as it has been possible to determine, the only variable in these experiments is that stated, and I am led to the conclusion that the conditions surrounding and incident upon the germ cell at the time of fertilization may be to a very considerable extent responsible for the determination of the dominant character in the cross and largely responsible for variability of such characters.

In Exp. No. H 701 B the behavior, where the recessive appears as a pure breeding race in F_1 , while by no means unique, is difficult of explanation on the factor hypothesis as at present understood.

It could not for a moment be maintained that external conditions are alone responsible for the determination of dominance or recessiveness, because it would be about as far from the truth as it is possible for one to get. External conditions have the same role in organisms that they have in any physico-chemical process, of accelerating, retarding, or changing the direction of the activity or of the reaction which is going on. The fundamental reaction in any of these hybrid crosses is that which goes on between the two physico-chemical complexes comprised in the combining germ cells. What that action actually is, is at the present time absolutely unknown. That it is due to combinations of the pangenes or biophores is a preposterous idea, and that a given ferment, a chromogen, of itself, or represented by any specific substance, is present as an entity in the germ cell is

likewise very doubtful. All that we are entitled to declare or believe on the basis of present actual evidence is that some condition in the physico-chemical constitution of these germ cells is present, that makes possible the appearance of one or the other of the two necessary factors which in many instances must be present in later ontogenetic stages, in order to produce a given result.

Relation of External Conditions to Dominance.

The question of dominance, while a vital one, has been somewhat wrongly attacked. I would hardly wish at the present time to attempt to account for the highly variable results that have been found in the dominance and recessiveness of characters by such explanations as germ contamination, variable potency, alternative dominance, or different types of latency, etc. It may well be true that there is variable dominance, but to what is this dominance due? It seems that many of the experiments in which variable dominance has been found and described were uncritical, and were carried on under the uncontrolled conditions of most breeding operations. In regard to variable dominance or alternative dominance, as a function of the gametic constitution of organisms, it is necessary that the operations should be carried on in such a way that surrounding or incident conditions are eliminated to the fullest extent; and experiments must be based, not upon one series, but upon parallel series of similar cultures. As far as Shull's (1908) attempt to explain this condition by various types of latency is concerned, there again the relatively gross conditions under which we are obliged to carry out most of our experiments leaves one open to criticism as to what the results observed were actually due. In other words, the question of dominance, as Bateson (1902) has suspected, is not entirely one of gametic constitution, nor is it one of external conditions, but it is a combination of the two, and this result seems to be fully borne out by the experiments cited in this paper.

Concerning the nature of the products which result from a given cross, much depends upon how dominance works and what it is that is present in the germ cells. The products

may well be modified and lead to endless confusion by this very fact which I have established, of the determining and influencing of dominance by external conditions. Thus, for example, in Exp. No. H 410, external conditions determined the whole future history of that culture. By the conditions surrounding the germ cells at the initial cross the total character of the race was determined for as many generations as I cared to continue the experiment. If this is generally true, and I see no reason why it may not be, then the determination of dominance, which determines also the resulting products, is a most vital factor in evolution.

Again, the variability in products which one finds, as, for example, the differences which MacDougal (1905) found between crosses of *Oenotheras* made by him in New York and those made by DeVries in Holland, when they were using, as far as could be determined, identical material, has a very direct bearing upon this point. MacDougal says: ". . . , the very differences between the results of the hybridizations, as carried out in Amsterdam and New York, suggest that the manner in which the various qualities in the two parents are grouped in the progeny might be capable of a wide range of variation. Many indications lead to the suggestion that the dominancy and prevalence, latency and recessivity of any character may be more or less influenced by the conditions attendant upon the hybridization; the operative factors might include individual qualities as well as external conditions."

This at once suggests differences in results, and difficulties that will arise through the carrying out of like experiments under unlike conditions. This phase of the situation is set forth to some extent in the second part of this paper in the experiments in synthesis. These experiments, while not susceptible of analysis along certain lines, indicate very clearly that the operation of the principles of alternative inheritance will be productive of diversity of results under diverse conditions when using homogeneous materials. This gives a clue which may be of paramount importance in the further investigation of the problem of the origin of species in nature.

In many organisms there exists a physiological isolation, which,

although the organisms may be close together, living in the same location, etc., by definite limitations in their reproductive activities prevents them from intercrossing. This may be due to incompatibility between germ cells, but quite often it is due to difficulties incident to copulation or to the penetration of sperms; that is, the difficulties are purely mechanical. Thus it might well rarely happen that an individual would arise of a character such that a cross could result; and if such a cross were made, a race having the attributes of one organism with the capacity for physiological isolation of the other, might easily arise and keep it from any further chance of intercrossing with other species.

CONCLUSION.

The experiments and observations herein given warrant the general statement that conditions external to a cross are important factors in determining the results thereof. This conclusion has been worked out in both normal and hybrid crosses, in crosses between races which have been created selectively, and between forms which arose as sports; and the second series of experiments in synthesis is sufficient warrant for attributing to this factor a considerable importance in evolution.

Underlying these, there are, of course, deeper factors than those with which we are dealing. The characters which behave Mendelianwise are in the main superficial, unimportant attributes of the organism, and only rarely are they the characters which would make for success or failure in the struggle for existence; they are most often color and specific characters, which, while fixed and vigorous in their behavior, are not important in the economy of the organism. These behaviors, beyond any question as to how and why, suggest the operation of something which gives a result best described at present in factorial terms; and that there are such things as later ontogenetic factors seems highly probable in many cases and absolutely certain as regards many colors. The knowledge that we have concerning melanogenesis leaves us no alternative in this respect.

Back of all this, however, is the fundamental question of how these germ cells, how this living substance is constituted, and what

is the relation in this complex of that which makes for the elaboration of tyrosin and tyrosinase in melanogenesis. What is it in this complex that localizes in a definite area the appearance of a pigment? What is it that combines into a definite pattern a series of attributes, some of which can be shifted and rearranged in the processes of hybridization? The problem of the constitution of the gametes of that which makes for form, for localization, for pattern, etc., is the fundamental problem; and as long as we fail to see clearly what the constitution of living matter is, such phenomena as these which we have been discussing must remain more or less superficial in our knowledge of the living organism.

There is nothing in the behavior of these attributes, in our ability to shift them and make new combinations, which, of necessity, commits one to any of the doctrines of preformation in pangenes or biophores, or to oneness of constitution and orthogenetic destiny. The situation, as regards alternative behaviors, should be free from the bias of biological orthodoxies, and to regard the organisms with which we are dealing as so many complex physical substances whose composition we are investigating, and among which we are seeking to determine the limits and laws of combination, will give the most rapid progress towards the end of a better understanding of the larger problems of the evolution of living substance.

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April 1, 1910.

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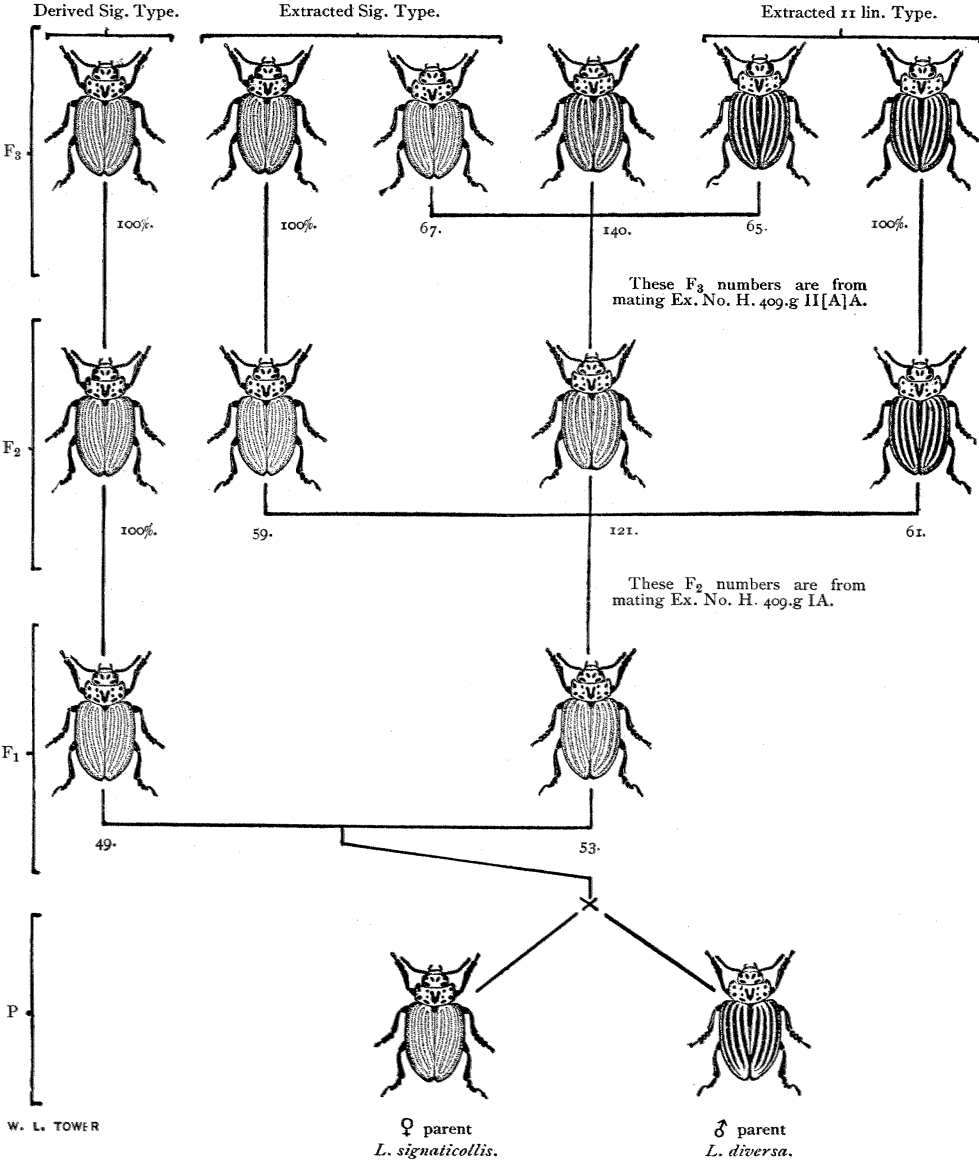
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EXPLANATION OF PLATE I.

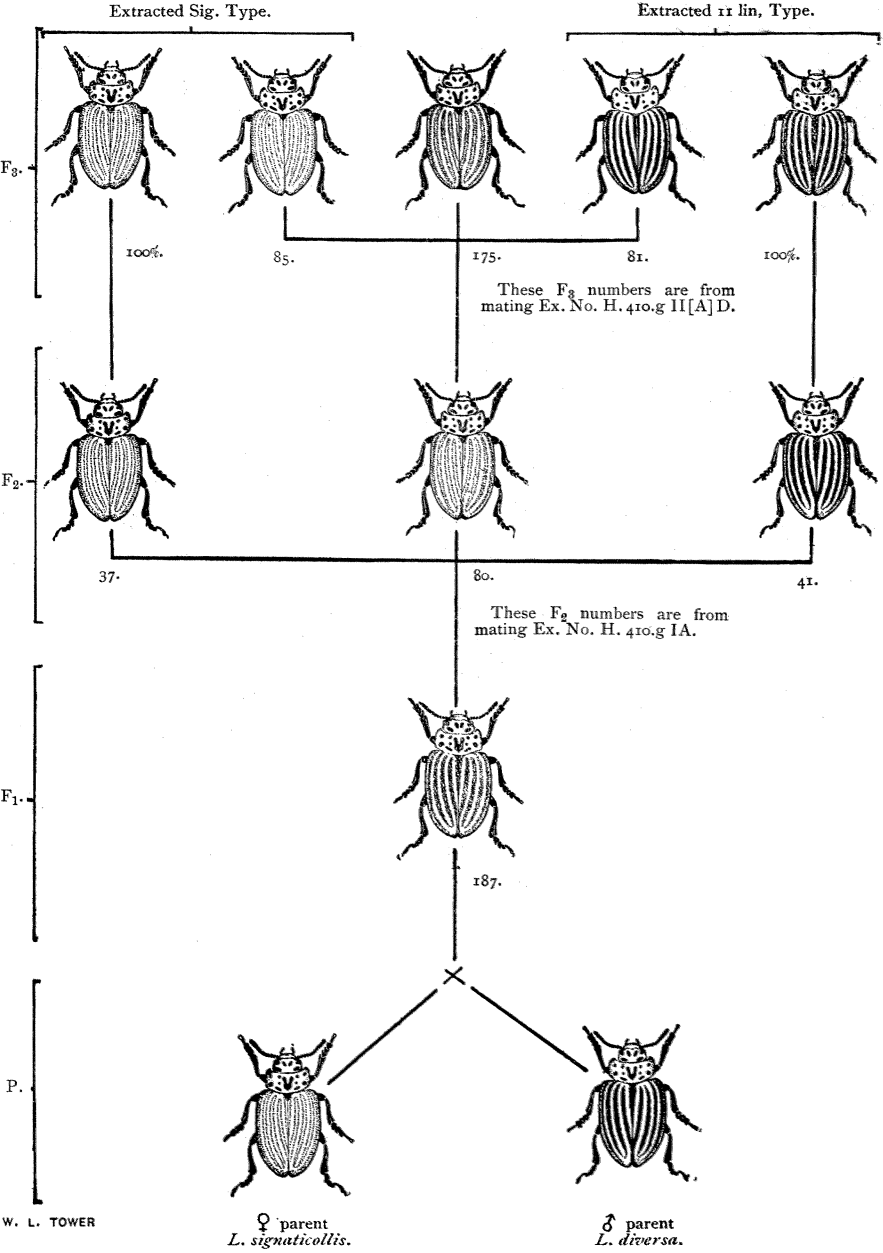
Note.—On all of the plates the pattern of the head and pronotum are not drawn with the true pattern and behavior which these cultures showed. The pattern shown is a basal one common to all the species.

Arranged to show the results obtained in crossing *L. signaticollis* ♀ × ♂ *L. diversa* under the conditions of Exp. No. H 409.



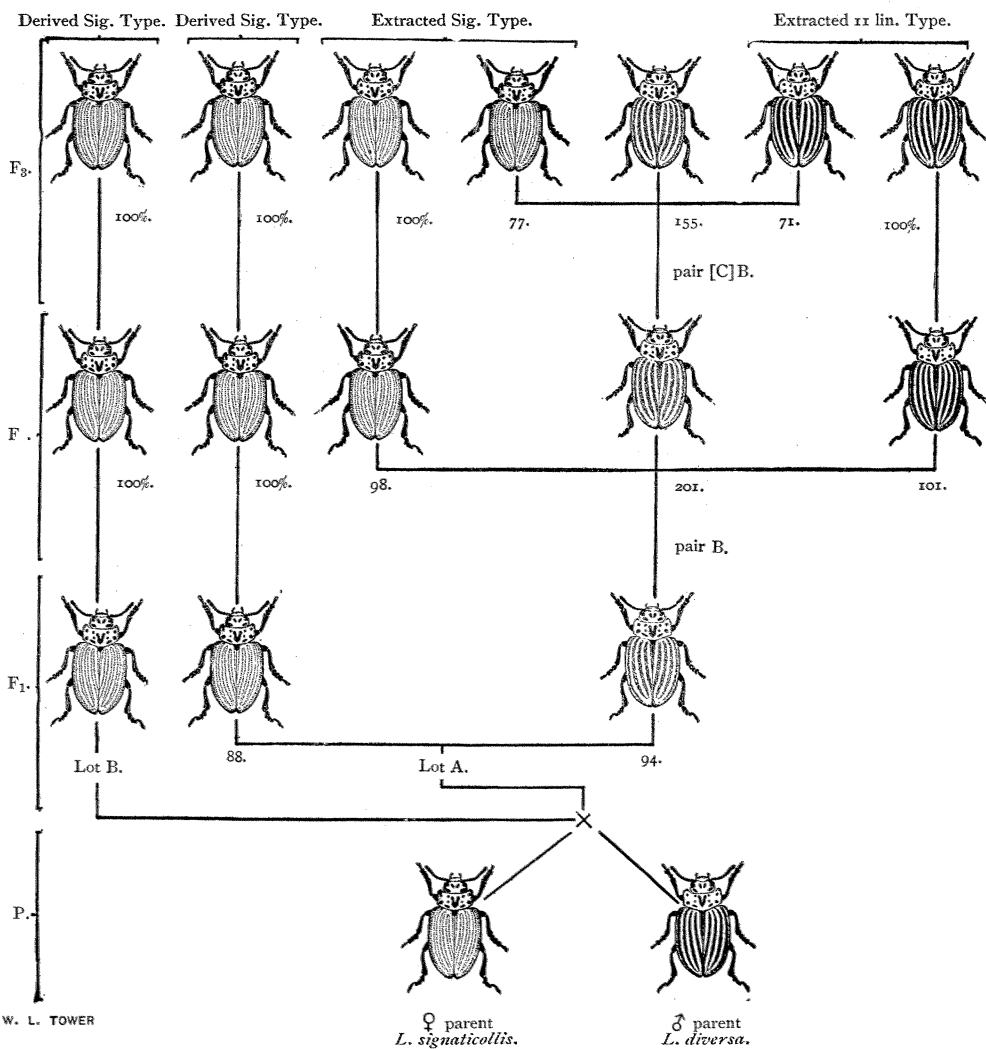
EXPLANATION OF PLATE II.

Arranged to show the results obtained in crossing *L. signaticollis* ♀ × ♂ *L. diversa* under the conditions of Exp. No. H 410.



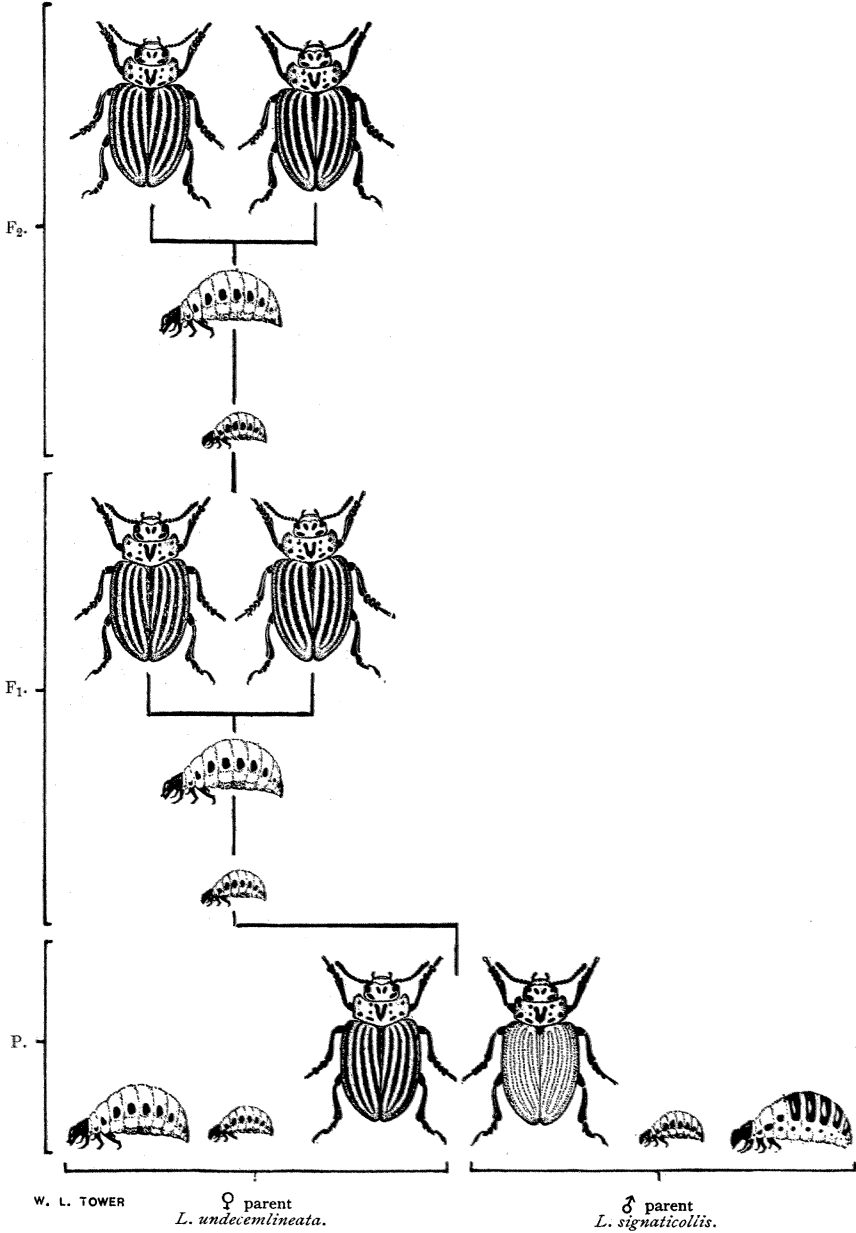
EXPLANATION OF PLATE III.

Arranged to show the results obtained in crossing *L. signaticollis* ♀ × ♂ *L. diversa* under the conditions of Exp. No. H 409 411.



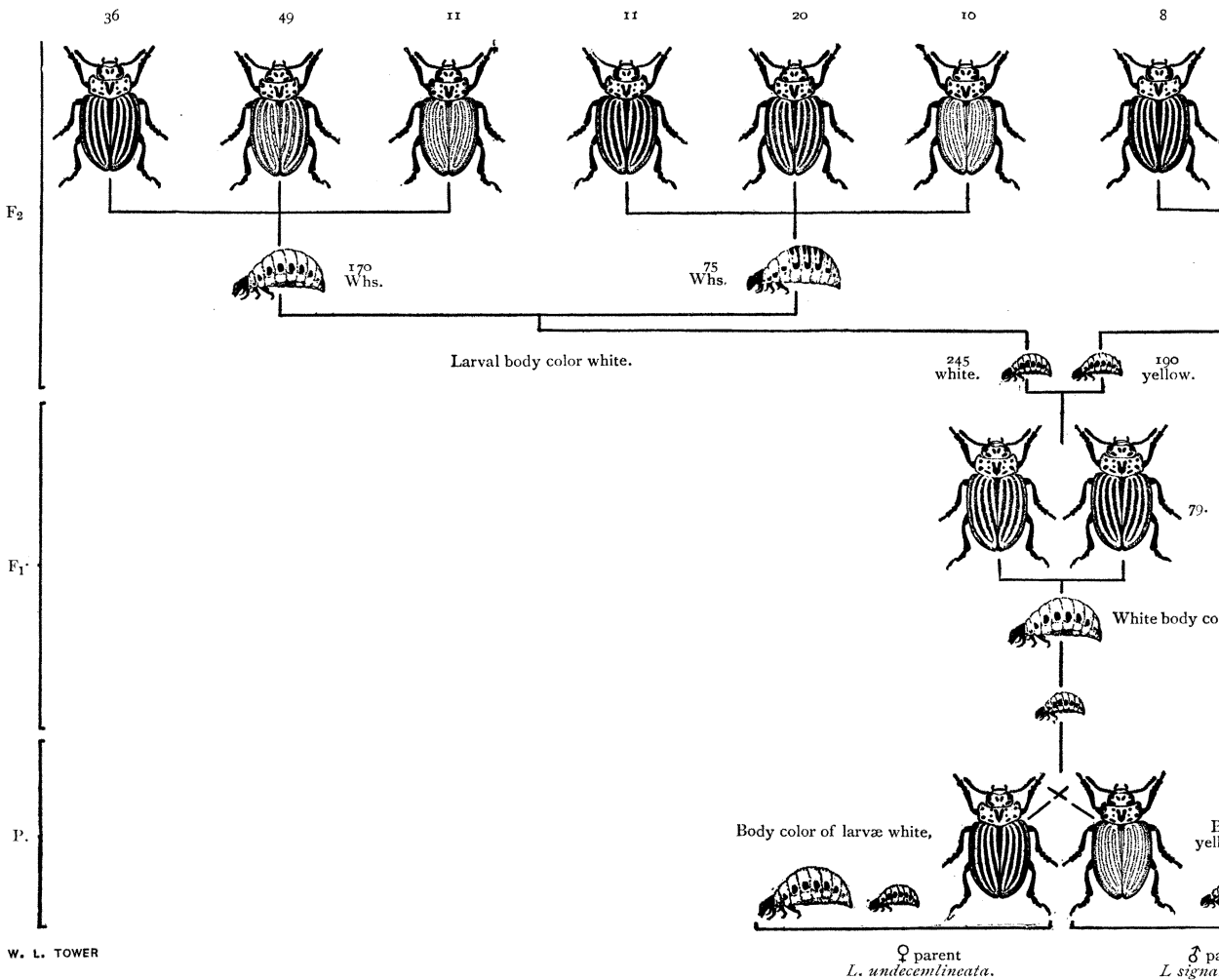
EXPLANATION OF PLATE IV.

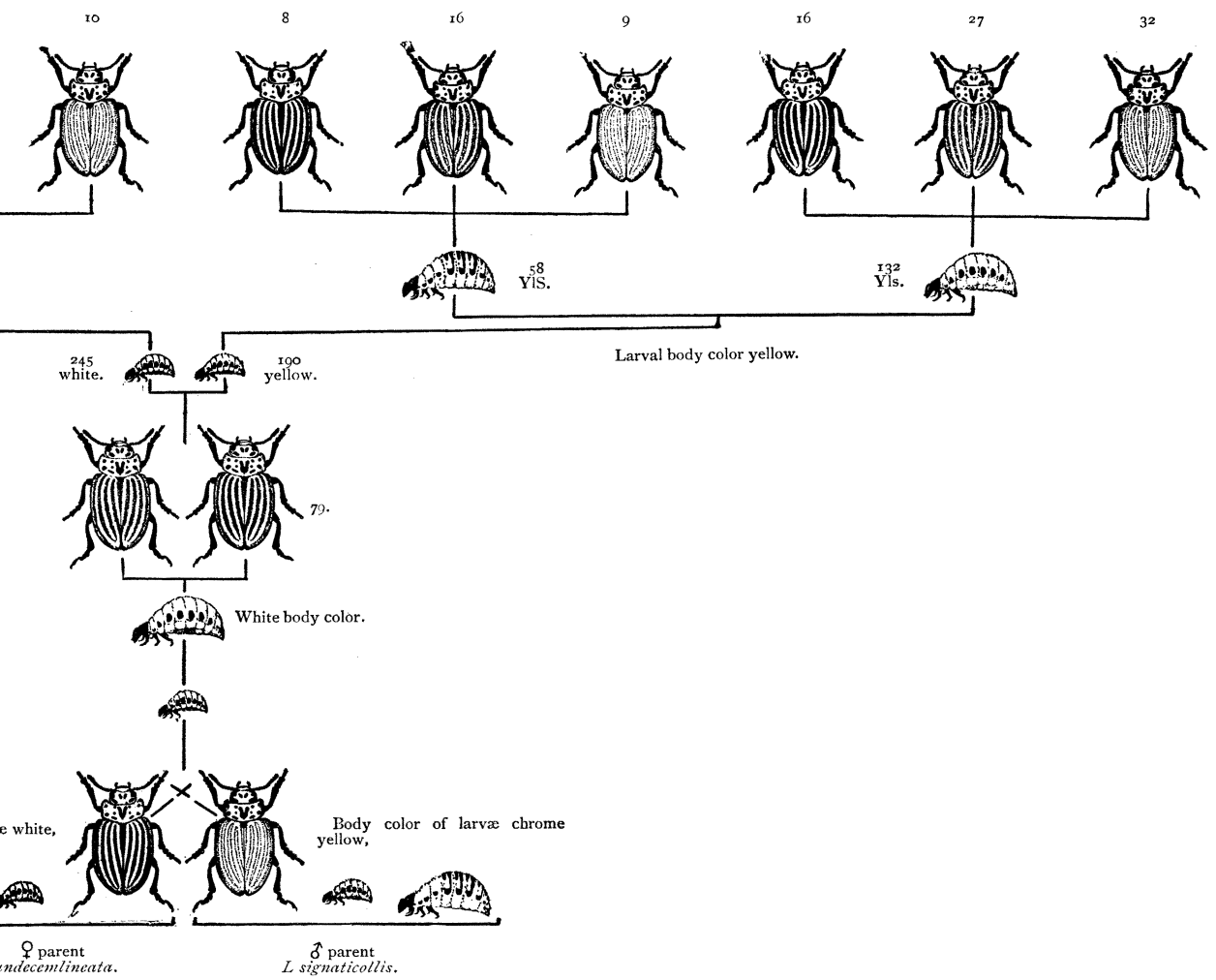
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L. signaticollis under the conditions of Exp. No. H 700 A.



EXPLANATION OF PLATE V.

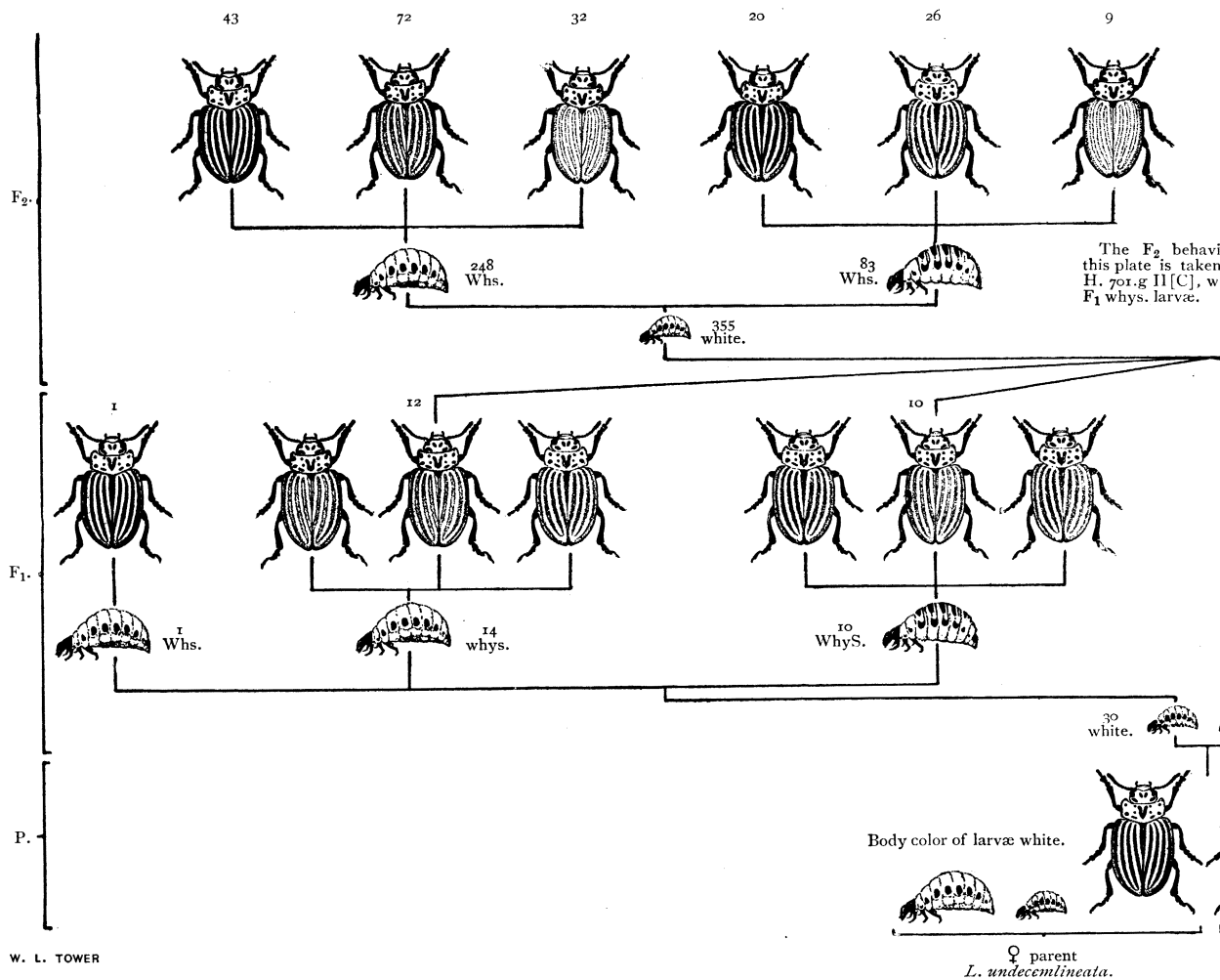
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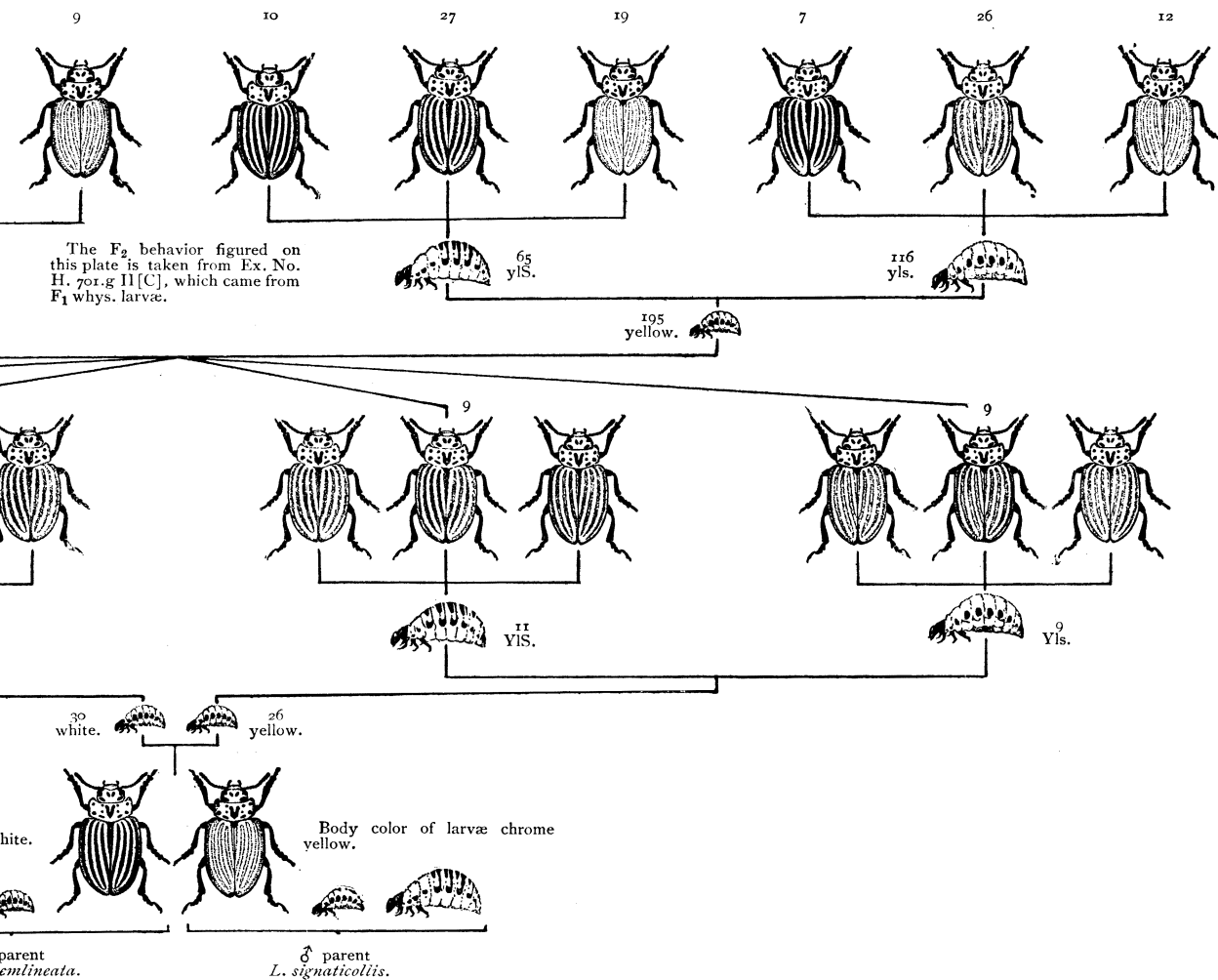




EXPLANATION OF PLATE VI.

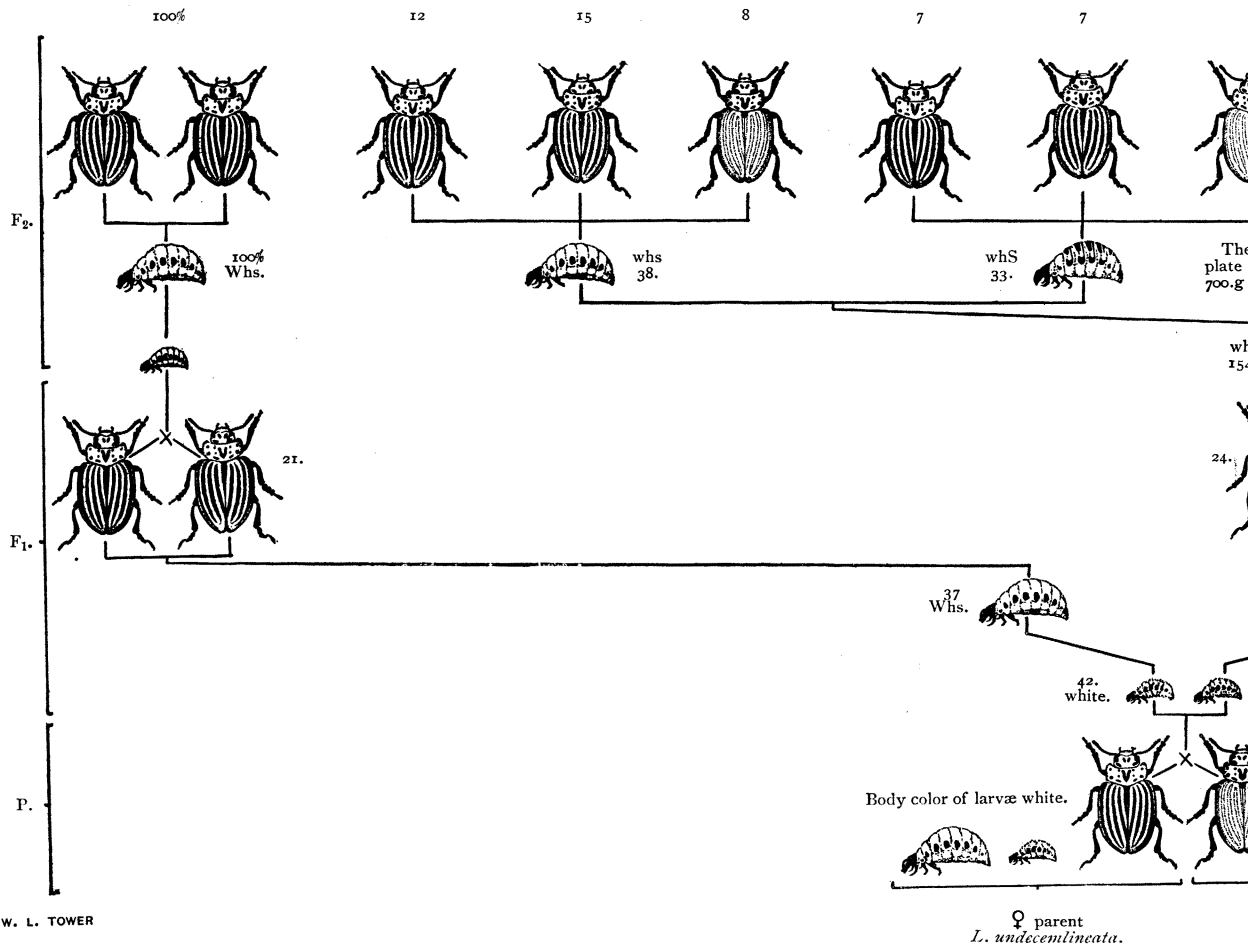
Arranged to show the results obtained in crossing *L. undecimlineata* ♀ × ♂
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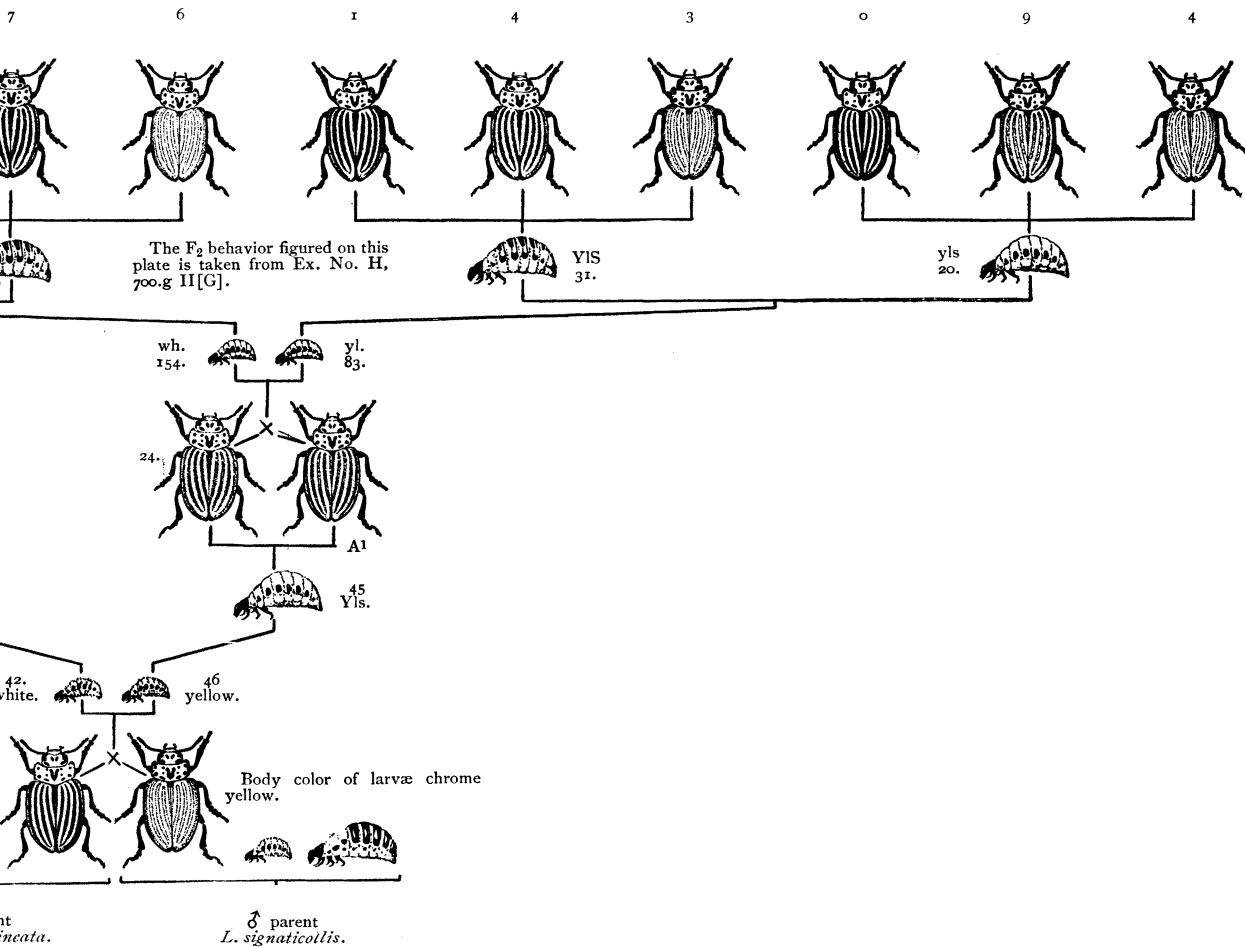




EXPLANATION OF PLATE VII.

Arranged to show the results obtained in crossing *L. undecimlineata* ♀ × ♂
L. signaticollis, under the conditions of Exp. No. H 700.





EXPLANATION OF PLATE VIII.

Arranged to show the results obtained in crossing *L. undecimlineata* ♀ × ♂
L. signaticollis, under the conditions of Exp. No. H 701 B.

